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Behavior of the red-footed booby (*Sulasula*) in British Honduras

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Behavior of The Red-Footed Booby (Sula Sula)
in British Honduras

VERNER

**BEHAVIOR OF THE RED-FOOTED BOOBY (SULA SULA)
IN BRITISH HONDURAS**

A Thesis

**Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science**

in

The Department of Zoology

**by
Jared Verner
B.S., Washington State College, 1957
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ABSTRACT

During three months of the breeding season in a colony of 3500 Red-footed Boobies (Sula sula) on 45-1/2-acre Half Moon Cay, fifty miles east of Belize, British Honduras, that species' little-known breeding activities were investigated.

Feeding flights of boobies began leaving the cay before daylight and returned in the evening until after dark. Wind direction and velocity notably affected the mode of the birds' departure but little affected their direction. Average flight-unit size was 2.41 birds. Contrary to published accounts, the boobies were able to take flight from the ground.

Displays associated with territorial ownership and pair-bond maintenance were noted and described, as were vocalizations. Apparently the males selected the territory, the females initiated nest construction, and each sex performed separate tasks in building the nest. The 44-1/2 days of incubation were shared equally by the sexes, as were the responsibilities of rearing their single young. The simple exchange at the nest normally occurred in the evening with each adult remaining at the nest a full day without eating.

Nestless pairs maintained territories, indicating that they do so year-round and that the pair-bond is sustained or life-long.

Young were fed by regurgitation, and they continued to depend on the adults for food until after they could fly. About a month before

fledging, the young disassembled their nest.

Inconsistencies with published material were noted in regard to such things as determining the stage of incubation of eggs on the basis of the condition of the nest lining, the condition of young when hatched and their subsequent development, and relationships between the boobies and Magnificent Frigate-birds (Fregata magnificens).

INTRODUCTION

The Red-footed Booby (Sula sula Linnaeus) occurs on isolated islands throughout the tropical world, situations where prolonged studies are undertaken only with considerable expense and difficulty. As a result, no one had ever attempted a continuous, extended investigation of these boobies, and practically nothing has been published on their behavior. The birds nest in large colonies; so data on the activities of many pairs can be collected with relative ease and rapidity. Since I had only a limited time for my study, the latter point was a very important one.

Fifty miles east of Belize, British Honduras, on tiny, palm-crowded Half Moon Cay, a colony of more than 3000 Red-footed Boobies has been established for over a century. The birds' nesting season there begins in early November and lasts for nearly eleven months; and each individual pair is engaged in nest building, incubation, and rearing of their single young for about six or seven months. Most pairs lay during December and January, and young begin hatching in early January. I was on Half Moon Cay for a period of three months, from February 14, to May 9, 1958, and during this time I made an intensive study of the behavior of the Red-footed Booby. There were numerous young of various ages, many unhatched eggs, and just a few empty nests when I arrived, and none of the young birds were yet able to fly.

The following account deals briefly with the physical description and distribution of the species, but the principal aim of the report is to analyse in detail my data concerning flight and nesting behavior. Other characteristics of the species, for example vocalization, are included as necessary parts of other behavior patterns. Certain phases of the life history will be touched on only briefly or not at all, since my study encompassed only part of an annual cycle. Data on plumage development and growth of young, which constitute a considerable portion of my field notes, will not be discussed fully here. However, that material will soon be prepared for publication.

STUDY AREA AND METHODS

Half Moon Cay, Figure 1, is one of three major islands on Lighthouse Reef in the Caribbean Sea, fifty miles east of Belize, British Honduras. Lighthouse Reef is the easternmost member of a group of coral reefs beyond the extensive barrier reef shielding the coastline of the Yucatán Peninsula and extending down along the northern coast of Honduras. Unknown to most people is the fact that this is the second largest barrier reef in the world. Between Lighthouse Reef and the barrier reef is Turneffe Island, a large atoll shown on most maps as a solid island. Actually, however, it consists of a narrow ring of land with a few passages and an interior lagoon crowded with a maze of islands and emergent stands of mangroves. Turneffe is about midway between Belize and Half Moon Cay and may be used as a reference point; since it is named on most Central American maps, whereas Half Moon Cay is not.

Half Moon Cay is small, being only 0.71 of a mile long and including only 45-1/2 acres. The eastern half has been cleared and planted with rows of coconut palms (Cocos nucifera). The ground beneath the palms of that section is composed of the cleanest, whitest sand I have ever seen. It is on that half of the island that the people live, and one of the houses is nearly half way between the ends of the cay. That house roughly marks the boundary between cleared and

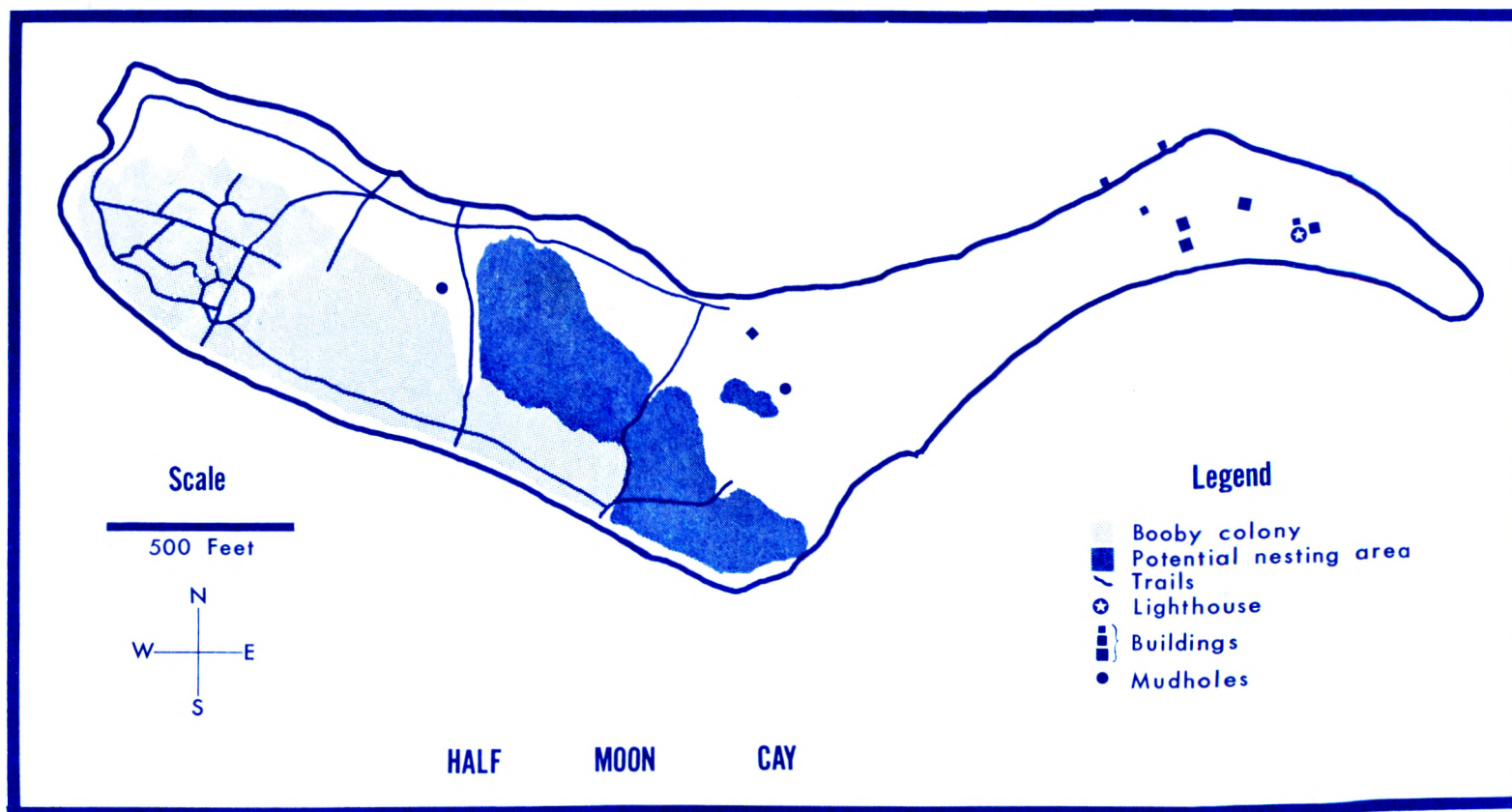


Figure 1. Half Moon Cay. The area outlined by white dots is shown in detail in Figure 8. The larger white dot within that area marks the location of my observation platform.

uncleared portions of the ground. Coconut palms are distributed profusely and randomly on the remainder of the island except in those areas, shown on the map, which support broadleaf trees. The floor of the uncleared palm grove has a mat of the procumbent, purple-flowered species, Ipomoea pes-caprae, with scattered patches of the conspicuous white lily, Pancratium littorale. A white-flowered, creeping plant contributing to the floor mat along the northwest side of the cay is Calonyction aculeatum. Other species occurring generally beneath the palms, mainly in spots relatively clear of the Ipomoea mat, are Ageratum maritimum, Alternanthera ramosissima, Rivina humilis, Stachytarpheta jamaicensis, Sida acuta, and Hamelia patens. The latter two species are confined to the moist, shady areas bordering the broadleaf tree stands. Wedelia trilobata replaces Ipomoea as the principal ground cover in sandier soil at the eastern border of the uncleared section and forms a dense mat near a mudhole in the center of the island. Erithalis fruticosa occurs only in association with Wedelia. A few scattered individuals of Erithalis spring from the Wedelia mat, and one large clump nearly eight feet high grows near the central mudhole. Tournefortia gnaphlodes grows only on the outer edge of the other vegetation and occurs around the shore of most of the uncleared section as well as on the easternmost tip of Half Moon Cay. Often associated with this soft green shrub are clumps of Pancratium.

In the booby colony there are just a few coconut palms and an abundance of broadleaf trees. There is virtually no ground cover

beneath the trees there, apparently because the ground is composed mainly of coral stones with only a little soil and humus in spots. The only plant with extensive distribution in the booby colony on which the boobies did not nest was Capparis flexuosa. This is a night-flowering bush that forms dense tangles of stems throughout most of the central section of the nesting colony. It was the greatest obstacle to trail clearing, and I dubbed it "tangle-foot." The principal tree, both in numbers and in utilization by the boobies, is the red-flowered Cordia sebestena. It is the only tree that occurs in all sections of the colony and the only one growing next to the shore. Most individuals are about twenty to twenty-five feet high, but some attain thirty-five feet.

Bursera simaruba occurs generally in all areas of the colony except along the shore, and Bumelia retusa occurs in all areas except along the shore and in approximately the eastern fifth of the colony.

Ficus sp. is distributed like Bursera but is much less common.

Pithecellobium keyense grows only in the central portion of the colony near my observation platform. Neea choriophylla is a very rare species in the colony, if rare is a proper term in the case of such a limited area. I was aware of not over five individuals of the species on the island, and all but one of those were in the eastern fifth of the booby colony.

Ximenia americana is also rather uncommon and is restricted to the northwest quarter of the colony. Pouteria campechiana is one of the principal species along the north border of the eastern half of the colony, where it occurs in association mainly with Bursera and Ficus. Those

three species reach heights of forty and fifty feet in that section of the colony, and they are the principal species composing the remainder of the broadleaf grove where the boobies do not nest. There were no mangroves on the cay when I was there, but Salvin (1864) said there were a few in 1862.

The cay is fairly barren of wildlife with the exception, of course, of the boobies and Magnificent Frigate-birds (Fregata magnificens). The only mammalian species on the island is Rattus rattus, which, according to the local word-of-mouth history of Half Moon Cay, invaded the cay from a wrecked ship during the nineteenth century. Today, the uncleared section of Half Moon Cay is thickly populated with rats, which cause a great deal of damage by nipping off coconuts and chewing into their centers. I recorded 98 species of birds on Half Moon Cay while I was there, and at least 77 of those were migratory forms. Seventeen of the migratory species were recorded regularly enough to indicate that they winter on or near the cay. Only two species, Sula sula and Fregata magnificens, were nesting at the time of my visit, and probably both the White-crowned Pigeon (Columba leucocephala) and the Groove-billed Ani (Crotophaga sulcirostris) nest there later in the year. I doubt that other species breed on Half Moon Cay.

A number of small lizards have found their way to the cay, including Anolis sagrei, Anolis allisoni, and Phyllodactylus sp.; and two larger species occur and provide an awesome part of the natural setting. The larger of the two is known locally as "Iguana" (Iguana

iguana) and the smaller as "Wish-willy" (Ctenosaura similis). George Young, senior light keeper at Half Moon Cay, has seen the Wish-willy take his chicks from beside the hen, run up a palm, and eat them; and various people in British Honduras have told me the large lizards eat the eggs and young of the boobies. I never saw either the Iguana or the Wish-willy eat anything but leaves and flowers; and I doubt that they ever take an egg or young of the booby--not only because they are principally vegetarian, but also because the adult boobies remain at the nest constantly until the young are large enough to defend themselves. Adults and young alike fiercely resisted the intrusion of their territories by Iguanas and Wish-willies.

The Hermit Crab or Soldier figures prominently in the booby colony and might best be characterized as the island's janitor. These animals are very abundant; in moist places they cover the ground so thickly that foot space is difficult to find! They eat nearly anything, including dead birds, lizards, etc. They also eat the fish regurgitated onto the ground by excited boobies as well as the excrement of the birds. This latter activity of the Soldier, combined with the porous substrate and high annual rainfall on Half Moon Cay, accounts for the absence of guano accumulation in the booby colony.

The climate at Half Moon Cay is generally mild; although the high humidity makes even slight temperature differences more noticeable. From March 20 through May 7, I recorded the temperature three times daily--between seven and eight in the morning, near noon, and between

seven and eight in the evening. These data are summarized in Table 1. The only hard rain on the cay while I was there fell on February 19, which was the only day with precipitation during the last half of that month. It showered four times during March, three times during April, and only once in the first seven days of May. Table 2 shows the rainfall at Belize since 1919. Although these records were taken fifty miles away, they are probably indicative of the conditions existing on the entire coast and on all the cays of British Honduras. Notice that the "dry season" extends roughly over February, March, and April--almost exactly coinciding with the study period.

There is nearly always a moderate easterly breeze across Half Moon Cay. It not only mitigates the effects of the high humidity, but it also keeps the entire island practically free of small flying insects. Since there are no swamps on the cay, there are few places for mosquitos to breed, and the island is virtually free of them. Only when the wind shifts to the west to carry mosquitos from Long Cay, an island with mangrove swamps lying four miles west of Half Moon Cay, does Half Moon suffer from that pest.

Hurricanes have crossed the cay only a few times, but their effect has been notable. Reference to the map of Half Moon Cay will show that the 85-foot lighthouse is near the south shore of the island. In 1848, the lighthouse was built midway between the north and south sides. By sweeping sand and coral from the south side across to the north side and there depositing it, the hurricanes have actually moved Half Moon Cay

AVERAGE TEMPS.	MARCH	APRIL	MAY
a.m.	79°	82°	83°
noon	84°	87°	88°
p.m.	81°	83°	83°
TEMP. RANGE	73°-89°	77°-89°	81°-90°

**Table 1. Temperature at Half Moon
Cay in degrees Fahrenheit.**

MONTH	MAXIMUM (YEAR)	MINIMUM (YEAR)	AVERAGE
January -----	11.19 (1921) -----	.84 (1945) -----	5.23
February -----	6.49 (1947) -----	.00 (1958) -----	2.44
March -----	3.95 (1937) -----	.00 (1948) -----	1.53
April -----	7.25 (1919) -----	.00 (1955) -----	2.02
May -----	13.23 (1933) -----	.06 (1947) -----	4.12
June -----	22.32 (1956) -----	2.11 (1927) -----	8.08
July -----	11.98 (1936) -----	2.68 (1923) -----	6.43
August -----	15.49 (1945) -----	2.05 (1957) -----	6.59
September -----	20.18 (1925) -----	2.91 (1923) -----	9.24
October -----	36.37 (1931) -----	1.99 (1923) -----	12.15
November -----	25.72 (1942) -----	1.27 (1939) -----	8.22
December -----	21.44 (1929) -----	1.80 (1928) -----	7.38
Annual -----	113.33 (1929) -----	42.03 (1923) -----	73.26

Table 2. Rainfall, in inches, at
Belize, British Honduras, since 1919
(from weather bureau records in Belize).

northward while not affecting the position of the lighthouse. At Northern Two Cays, eighteen miles north of Half Moon, the lighthouse has been left behind by the shifting cay, and a concrete walk at least 150 feet long has been built to connect the lighthouse with the island. According to George Young, the hurricane of September, 1931, wiped out about half the existing booby colony, and the birds have not yet returned to their former numbers, although they are increasing.

On February 16, I began a systematic count of the nests in the booby colony. In the area to the west of the path that crosses the colony, I cut a network of trails separating that section into smaller units. Each tree containing a nest was tagged. On the tag was recorded a number for the tree, the species of tree, the date, the number of nests in the tree, and the contents of as many nests as I was able to examine. The same information was recorded in my notebook for future reference. East of the bisecting trail, I ran strings to separate the area into narrow strips. Then I worked slowly within each successive strip counting and recording the number and species of trees with nests and the number of nests in each tree. The trees in the eastern half of the colony were not tagged, so the western half became my principal study area. On March 3, I completed the nest count with a total of 1389 nests. Working from that figure and considering the large number of nonbreeding individuals present, but not counting the nestlings, I estimated there were approximately 3500 Red-footed Boobies on Half Moon Cay at the time. Of that number, probably 500 were immature birds that roosted in

groups in various sections of the colony.

By using a mirror attached to the end of a fifteen-foot pole, I was able to examine rapidly and safely from the ground most nests in my study area. The ideal type of pole for this purpose is an aluminum pipe with detachable sections, which can be made considerably longer than fifteen feet and still be light enough to handle with relative ease, whereas a wooden pole fifteen feet long is near the limit for satisfactorily handling. A platform (see Figure 8) was constructed at a location ten feet up in a Ficus from which I could observe over 100 occupied booby nests. Several were within 25 feet of the front of the platform, and three were in a tree above and behind it, not more than eight feet from where I sat. The birds have little fear of man, so it was unnecessary to construct a blind on the platform. However, I put a palm-frond roof on it to provide shade. At the time I chose a Ficus for my platform, I was unaware that it was the only satisfactory species of tree for that purpose in the colony. The other species were either too spindly or too brittle to be safe. In fact I later had branches of Bursera simaruba up to three inches in diameter snap off beneath only part of my weight!

Most of my observations on nesting behavior were made directly from the platform. Frequently I observed the birds' flight characteristics from the top of the lighthouse, from which I could also record the aerial combats between boobies and frigate-birds. Unfortunately I had

no wind recording equipment to use in conjunction with the flight studies. I will consider it as essential equipment should I ever again make such a study. One tool I found indispensable was a forked stick about two feet long that I used to force adults from their nest when I wanted to examine the nest's contents, and even then it was often a struggle to avoid their sharp, serrated bill. An aluminum step ladder would have greatly facilitated this work, since the nests at Half Moon Cay are so high. On most other islands of the world, apparently where the vegetation is not as tall, the boobies nest at lower heights; so in some colonies, a ladder might not be an essential item.

The accessibility, climate, and facilities of Half Moon Cay, and the size of the booby colony there combine to make the cay an ideal place to study the Red-footed Booby. Of all the colonies of Sula sula in the world, I doubt that any could be better suited to investigation than the one on Half Moon Cay.

DESCRIPTION AND DISTRIBUTION

Sula sula is a pantropical species with three presently recognized races. S. s. sula breeds in the Caribbean area and on a few islands of the tropical Atlantic. S. s. websteri is found on islands of the eastern Pacific off the coasts of southern Mexico, Central America, and northern South America. And S. s. rubripes completes the species' distribution about the globe, as it occupies the remainder of the tropical Pacific and the Indian Ocean. The distribution of the entire species is shown in Figure 2.

The variety of plumages described for the Red-footed Booby is undoubtedly one of the most confusing aspects of the species. Many of the phases have been described as distinct species; and, according to Murphy (1936), synonyms of the species include piscator, rubripeda, erythroryncha, brasiliensis, candida, hernandezi, coryi, websteri, autumnalis, and nicolli. In the Caribbean subspecies, two distinct color phases occur and interbreed regularly where they are found together. At Half Moon Cay, both phases are present. Tallies were kept of brown and white phase birds leaving the cay for the day's fishing on each of ten different mornings to give a total count of 3932 birds. Only 2 per cent were in the brown phase, and every brown bird I located on a nest was paired with a white one.

The proportions of white to brown phase vary among the populations

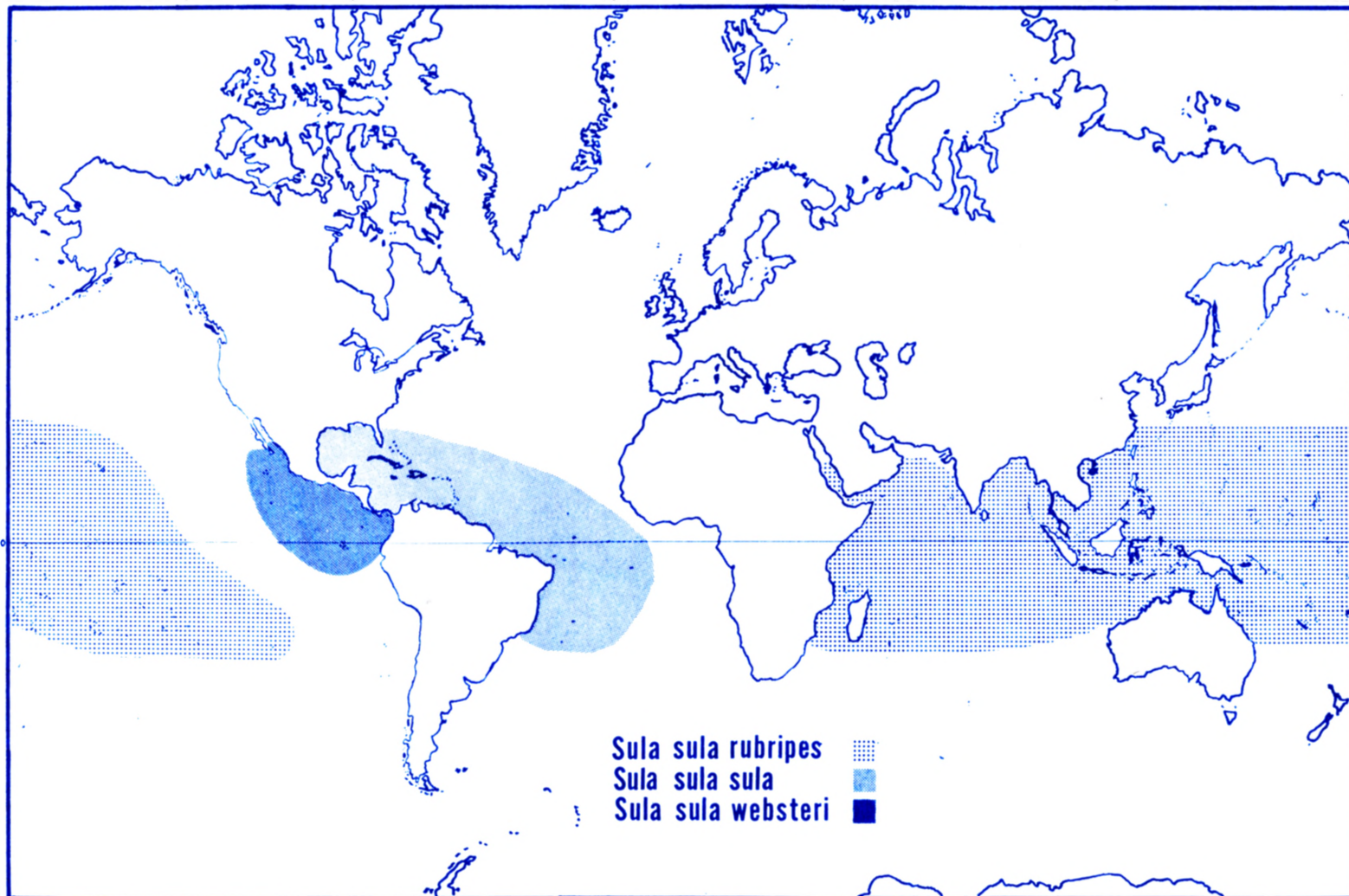


Figure 2. World-wide distribution of the Red-footed Booby.

of the world. The brown phase predominates on Venezuelan islands (Lowe, 1909), the Galapagos Islands (Beck, 1904), Howland, Enderbury, Palmyra, and Jarvis Islands (Munro, 1944), and Glorioso Island (Nicoll, 1906). On the other hand, Nicoll found white and speckled birds predominating on Assumption Island, just fifty miles from Glorioso. The white phase is also in the ascendancy on the Revilla Gigedo Islands (Beck, 1904) and at Moku Manu in the Hawaiian Islands (Munro, 1944). In addition to the brown and white phases, various intergrades between the brown and a so-called gray phase have been described for Pacific and Indian Ocean birds. Nevertheless, the white and brown phases seem to occur throughout the entire range of the species; and I think, like Murphy (1952), that the phases definitely have a genetic basis and are not simply age or sex differences. It remains to be answered why the proportions of phases vary so among the populations and why, as in the case of Glorioso and Assumption Islands, populations of brown and white phases can exist within fifty miles of one another without any apparent mixing between the populations. Only by a combination of plumage investigation and behavior study of several populations in different parts of the world could a satisfactory analysis of the phases be realized.

Besides the variations in plumage, the color of the irides of Red-footed Boobies differs, and some published accounts seem to be contradictory. At Half Moon Cay the irides of all the adults I examined were brown. Maynard (1889) reported that birds on the Cayman Islands had brown irides, and his colored figure bears that out. However,

Nicoll (1904) wrote that adults from the same colony had gray irides. Bannerman (1930) described an adult from Venezuela with dull yellow irides, while Murphy (1952) wrote that both the brown and the white phases on the Venezuelan islands have brown irides. It may be that Bannerman actually collected an adult Sula sula from Venezuela with yellow irides, since Fisher (1904) reported that Laysan birds have yellow irides. However the birds in most colonies of Sula sula apparently have brown irides.

The white phase of the Red-footed Booby is white throughout except for the brownish-black primaries, secondaries, greater upper wing coverts, and median under wing coverts of the manus. The white feathers, particularly those of the crown, nape, and back, have a variable straw-colored wash that I believe is a salt water stain. The brown phase is grayish-brown throughout except for the white lower back, lower abdomen, upper and under tail coverts, and tail. The remiges are brownish-black, and the same straw-colored wash noted in the white phase occurs in the brown. The fact that the legs and feet of both phases are orange-red accounts for the common name of the species. The pale blue bill and the colors of the naked facial skin are also the same in both phases; however, colors of the soft parts differ between sexes during the nesting season.

The colors of the soft parts assume their brightest shades near the time the egg is laid, so different pairs are brightly colored at different times. During most of the year, both sexes appear identical,

and no satisfactory color distinctions have been established between them. About half an inch of the base of the lower mandible is light pink, and usually a narrow strip of dull violet to dark bluish-purple (often appearing black from a distance) separates the pink section from the feather margin of the face. Occasionally the dark strip is entirely lacking. The pink color extends upward slightly onto the base of the upper mandible, and pink also colors the narrow strip of naked skin on the forehead and extends downward in front of the eyes in varying amounts. The naked skin around the eyes varies from dark to light blue, and the lower lid is marked with a whitish half moon, which is apparent only when the lid is closed. The color of the gular sac is probably the most variable; many descriptions ascribe black to that of the male and gray to that of the female. However, I found no such clearcut distinction at Half Moon Cay. From a distance, most males appeared to have black gular sacs and most females grayish ones. On closer inspection, however, I found that the sacs of both sexes had mixtures of brown, violet, purple, and pink. Depending upon the shades, some of the sacs were darker than others, resulting in apparent blacks and grays. I noted some males with "solid gray" sacs, some females with "solid black" ones, and both sexes with the area part gray and part black. I was unable to determine definitely any variations in the color of the gular sac depending on variations in the breeding condition of the birds, but I obtained limited data indicating that it darkens about the time of laying, especially in the males. Gibson-Hill (1948) reported that the interramal

skin of the Red-footed Boobies on Christmas Island in the Indian Ocean is normally blue-gray with a hint of mauve. He found that it darkened to dull purple, almost black, at the beginning of the breeding season, which suggests a sexual significance.

I made colored drawings of the faces of several birds and checked the birds at times thereafter to determine the degree and rate of any change in facial coloration. The pink and blue colors of the soft parts of the females were darkest and brightest at the time of laying, but no change in the basic colors was detected. On the other hand, the pink of the males was changed to orange, and the blue was changed to light green or bluish-green. The colors of both sexes began to revert slowly just after the time of laying; and both birds again appeared similar within six to seven weeks. During the changing stage, the colors of the males' faces graded from orange to salmon to pink and from green to blue; and those of the females' faces simply faded to lighter shades. Thereafter, when both sexes again appeared similar, there was no natural way to differentiate between them, except by behavioral characteristics. The pairs to which I devoted the majority of my observations were marked on their feathers with India ink in a solution of alcohol, which penetrated the feathers and gave a fairly permanent mark. The sexes of those pairs, then, were quickly distinguished in the field by their individual, artificial markings.

GENERAL BEHAVIOR

The Red-footed Booby, like pelicans, cormorants, and other boobies, is a fisherman by trade, and a very specialized one it is. Its primary food is the flying fish; squids are also taken in some parts of the world, as well as a variety of very small tropical fishes. The latter I found on the ground beneath a roosting tree of some immature birds. When Red-footed Boobies are violently disturbed, they regurgitate some of their stomach contents---a reaction accounting for most of my records on the diet of the species. However, in a very short time, the birds with which I was working daily became accustomed to my intrusions and no longer regurgitated. So it was not until May, when Linton Price and I began banding birds that I had not been disturbing daily, that I found anything other than flying fish in their diets. Most of the flying fish taken by the adults ranged between five and eight inches in length, but ten- and eleven-inch flying fish were also taken. Such a long fish must certainly extend part way up the esophagus of the booby before it is digested.

The boobies catch their food by diving vertically, with wings half-closed, into the sea; often they gather in considerable numbers over schools of fish. Bangs (1902) noted a feeding flock (identified as Red-footed Boobies, though no specimens taken and description incomplete) off the coast of Florida during a storm "every now and then collecting

over some school of small fish and diving from a height like a party of boys following each other off a spring-board." Ordinarily they dive from heights of fifteen to thirty feet. Gifford (1913) observed Red-footed Boobies catching flying fish on the wing by pursuing them when they left the water to skim along the surface. I observed the same behavior by an immature Brown Booby (Sula leucogaster) and a number of Pomarine Jaegers (Stercorarius pomarinus) off the east coast of Yucatán, Mexico but I never saw Sula sula engaged in the sport. Red-footed Boobies rarely feed actively near the nesting colony, so I had little opportunity to observe their feeding behavior. The only time I saw adults diving for fish was on May 3, when a merchant vessel passed about 1/2 to 3/4 of a mile east of Half Moon Cay with at least ten Sula sula diving at the bow for fish. I was observing through a 60X telescope but still could see very little. Frequently the boobies cruised around over the sea near the colony, apparently in search of fish, though I never saw one catch anything. Their normal pattern was to leave the island in the early morning, fish well beyond sight of the cay, and return late in the evening. Their activities in that respect will be analysed in the following chapter.

Boobies returning to their nests with fish ran the risk of being attacked by frigate-birds and forced to disgorge a part of their catch. That species of the genus Fregata employ aerial piracy to secure much of their food from smaller pelagic species is well known. However, as

far as I know, it has not been noted previously that apparently only the female frigate-bird engages in such maneuvers. In 86 recorded observations of these encounters, I failed to note male frigate-birds harassing boobies to obtain food. However, males were noted on several occasions chasing boobies to get nest materials from them. On the other hand, on March 27, I saw a group of boobies, varying from five to eleven, chasing a male frigate-bird that was carrying a stick, which they attempted to snatch from below. That encounter lasted at least four minutes with only three or four of the boobies actively trying to wrest the stick from the bill of the flying frigate-bird. Finally the frigate-bird dropped his stick, and one of the boobies caught it in mid-air.

When female frigate-birds chased the boobies to get fish, they never hesitated to follow them across the cay, down among the tree tops, and even to the boobies' territories, contrary to Maynard's (1889) report that the frigate-bird never pursues a booby over land at Cayman Island. Usually only one frigate-bird was involved in a given attack, but occasionally two, three, or even four teamed up after a single booby. Frequently they took the booby by its tail and up-ended it on the wing in an effort to make it disgorge, and less frequently a wing-tip was seized. Whenever a booby regurgitated some fish, the frigate-bird darted after it and either caught it before it hit the water or picked it off the surface. The boobies usually screeched loudly when they were attacked. But, in spite of the aerial disputes between the two species, they built their nests side by side and lived in apparent harmony while

at the nest. However, Brown (Devas, 1953) reported seeing frigate-birds at Giles' Rock, off Tobago, snatch eggs from boobies' nests after he had chased the boobies off and even from directly beneath sitting boobies! When the frigate-birds' eggs began hatching in early April, the number of attacks on the boobies increased.

Movements of Red-footed Boobies to a great distance from their home colony seem to be unusual and irregular, so a few records seem worthy of note here. To my knowledge, the only specimen taken in the United States was a juvenal, shot in southern Louisiana by J. N. McConnel on November 1, 1940. The colony of Red-footed Boobies nearest Louisiana is on the Cayman Islands, south of Cuba. Bangs (1902) recorded what was probably a group of Sula sula off the coast of Florida that may have come from Samana Island in the Bahamas. Munro (1943) reported recoveries of banded birds in the Pacific area 550 and 700 miles south of the banding station! And, finally, Tomlinson (1947) reported that thousands of Red-footed Boobies roost on the rocky cliffs of Ascension Island in the Atlantic during May and June each year. This last record is of particular interest, since it is the only hint that any Sula sula have an annual pattern of movement between areas. It is of further interest, because I know of no population in any part of the world known definitely not to be engaged in nesting activities in May and June, so the nesting site of the birds remains a mystery. The record certainly deserves further investigation.

Sula sula is a very inquisitive species and shows little or no fear

of man in its investigations. Farquhar (1900) had an interesting experience with Red-footed Boobies, especially the immatures, near Madagascar. He wrote:

One would hover above my head, just going fast enough to keep pace with the boat; it would examine with an apparently critical eye every detail, turning its head from side to side in a most comical way. If I put up my hand to catch it, it did not attempt to fly away, but would give a sort of squawk and peck at my fingers; there it would remain till driven off by another who wanted to look. There was apparently no reason for these attentions, as we were a mile from shore and in no way interfering with their domestic arrangements.

Anthony (1898) had Red-footed Boobies landing on his head and shoulders and on the rail of his skiff as he pulled ashore at San Benedicto Island in the Revilla Gigedos. And, in the Hawaiian area, they reportedly tried to take fish off the hooks of fishermen (Stejneger, 1889).

I was told that juvenal birds at Half Moon Cay frequently try to steal fish from the fishermen's boats; although I never observed such an attempt. The juvenals were by far the most inquisitive, frequently pausing on outstretched wings to examine thoroughly the mast of a sail boat or the top of the lighthouse. Linton Price told me of seeing eight or ten juvenals following a Snowy Egret (Leucophoyx thula) in apparent curiosity. During strong winds, adult and subadult boobies made a habit of forming small soaring parties above the windward shore in the early morning and late afternoon. On three such occasions, twice in the morning and once in the evening, I walked along the shore beneath the birds. They moved along just above me, looking down at me and

occasionally dropping to within twenty feet to get a better look. If I turned and walked back the way I had come, the birds continued to fly above me and followed me back. Back and forth they followed me as long as I stayed on the windward shore. Apparently the birds formed these soaring flocks simply for enjoyment and exercise; and whenever there was no strong wind they simply flew around over the colony and out over the adjacent water for a short time in the evening. I feel confident that most of the birds composing these evening flights were ones that had just been relieved, after a day of attending their nests, by their mates that had returned from the day's fishing.

FLIGHT

The flight of the Red-footed Booby is, indeed, a thing of grace and beauty. The birds fly swiftly and directly when they have a destination but tend to fly more aimlessly when fishing or cruising about over the colony in the evening. They take flight from the ground with difficulty, unless they can fly into the wind. Occasionally I came upon them on the trails of the colony. They jumped up and flew ahead of me, staying about a foot or two above the ground, until their wings became entangled in brush and they were grounded. Linton Price told me of one such bird that flew away from him just above the trail until it came to an opening in the vegetational canopy large enough for it to veer upward and away. When the birds were low in the shrubs, they lacked sufficient room in which to flap their wings and could not become airborne. So they climbed from branch to branch until they were high enough to clear the foliage. By hooking their necks over a branch above themselves--- often appearing to "hang" themselves---, bringing both feet up to grasp the branch, and pulling themselves onto the branch, the boobies climbed ably. If they were grounded near the shore, and I came upon them suddenly, they half ran and half flew toward the beach where they flew off easily on the wind currents. From the water, the boobies flew by jumping up and kicking backward into the water with both feet together in a manner similar to that employed by pelicans.

Several times I saw boobies gathering nest materials from the ground at the windward side of the cay; from there they flew with ease into the wind. Normally, however, the boobies seemed to avoid the ground. Only by some mishap were they ever grounded within the colony, and when a dependent young fell to the ground from its nest it was doomed. The adults would not go to the ground to feed their young, even when they could see them plainly from the nest!

The boobies fly alone or in small flocks, in which they tend to maintain an imperfect unison among themselves as they flap and glide intermittently. That is, one bird may begin to flap and the others follow suit, though not always instantly. In fact, some may continue to glide while the remainder flap, then flap while the others glide. But, on the whole, a single flight group tends to maintain an approach to unison in its flap-glide pattern. I would not say, however, as Clifford (1913) puts it, that members of a flock are "practically synchronous in every action." According to Traylor (MS, 1958), the boobies fly in small flocks of four to twenty birds. These figures most likely apply to flocks far out to sea on the fishing grounds, since the average size of 2192 "flight units" (defined later) that I observed leaving or approaching the cay was 2.41. These data will be discussed in detail below.

Wind and air currents are important factors in the flight of the species even after the birds have become airborne. I never had the opportunity to observe the active feeding behavior of the birds, since they rarely fed near the cay. But I did spend several mornings watching

them fly out to sea for the day's fishing. The importance of wind currents was very apparent when the birds glided out over the sea, rising and falling to meet each swell but never once stroking the air with their wings. I often saw them glide, seldom more than a foot or two above the water at any instant, for upwards of a hundred yards before flapping their wings again.

I have no way of knowing from personal experience what formations the birds tend to follow during their fishing excursions. Flock patterns have been described variously as lines and wedges (Maynard, 1889), but I never saw a distinct pattern in any flock during my three months at Half Moon Cay. Instead, disorder seemed to be the rule. On rare occasions the birds formed into irregular ranks or files, but they seldom held their positions more than a few seconds. Groups were constantly breaking up, reforming, and joining other groups. The largest single flock I saw consisted of 36 birds departing just before daylight for the day's fishing on March 5.

During morning and evening flights and not including midday counts, I recorded a total of 2148 "flight units" (the term "flight unit" being used here to designate any solitary bird or group of birds). The count included 1013 lone birds, and the average per unit was 2.40. The average size of units of three or more birds was 4.96. The largest flight unit included in the count contained 24 birds; the numbers of the various flight unit sizes are shown in Table 3. Counts were taken from a platform surrounding the top of the 85-foot lighthouse at the eastern end of

FLOCK SIZE	MORNING	EVENING	TOTAL
1	430	583	1013
2	249	263	512
3	119	123	242
4	60	77	137
5	45	31	76
6	16	34	50
7	11	18	29
8	10	15	25
9	6	13	19
10	4	10	14
11	2	2	4
12	3	3	6
13		5	5
14	3	3	6
15	1	1	2
16	2		2
17	1	1	2
18	1		1
19	1		1
20			0
21			0
22			0
23			0
24		2	2

Table 3. Number of flight units by size.

the cay, which was an ideal location for morning counts, since all departing birds passed within easy view. In the evening, many boobies approached the nesting colony from directions that did not bring them near the lighthouse. However, since the lighthouse was elevated, all the returning birds could be seen from it, and it was the best location for evening counts, although not as good as it was for morning counts. Records were kept in such a way that the number and size of the flight units in each fifteen-minute period could be computed. The fifteen-minute flight count periods were begun on the hour. As I was taking the counts I gained two clear impressions regarding the average flock size. In the first place, I thought that the average size decreased later in the morning during the departure flight and increased later in the evening during the return flight. Thus, the nearer the time was to the dark period, either at its beginning or its end, the greater the mean size of the units seemed to be.

That this was actually the case is demonstrated in Figure 4. The graphs in Figures 3 and 4 are based on time units of fifteen minutes as they relate to the fifteen minutes when peak numbers of birds were recorded. The counts ranged over a 66-day period; so the times of sunrise and sunset were much different between the first and last counts. By combining figures from all counts in terms of their relation to the peak flight period and not on a simple time designation, bias resulting from differences in times of sunrise and sunset has been eliminated. Notice that the average flight unit size dropped from 4.3 in the earliest

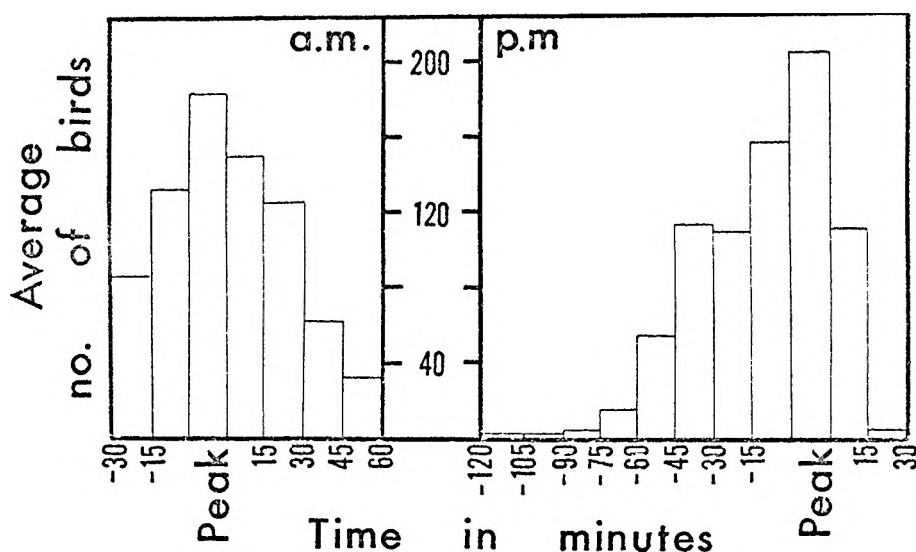


Figure 3. Average number of birds in flight count periods with counts totaled in relation to their peaks. Each count period lasted 15 minutes; times before the peak period have been given a negative value.

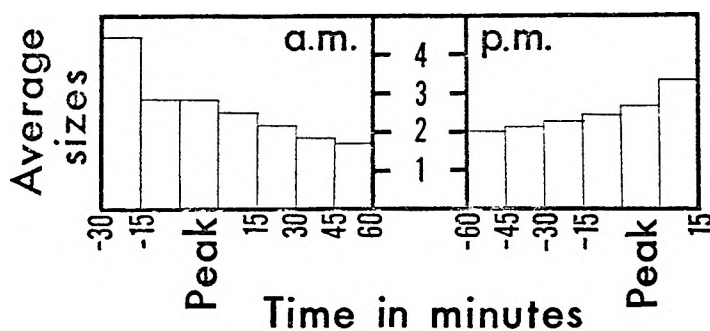


Figure 4. Average flight unit size by count period. The times designated in this figure correspond to the times in Figure 3, and a comparison of the two figures is essential for an understanding of Figure 4.

morning count period to 1.7 in the latest. And, in the evening, it rose from 2.0 in the earliest period with an appreciable count (discounting the first four periods in which too few birds were recorded to obtain satisfactory averages) to 3.2 in the latest.

In the second place, I believed the flocks averaged slightly larger during morning flights than during evening flights; however, this proved not to be true. In fact they proved to be insignificantly smaller---2.38 as compared to 2.41 in the evening. However, 4.3 was the largest average size during any morning count period compared to only 3.2 for the evening, a fact which may have given me the impression that morning flocks averaged larger than evening flocks.

Apparently there are fewer birds flying alone during periods with a high flight unit average, and the difference is distributed about equally among all the other flock sizes. In Figure 5 notice the wide discrepancies between the numbers of flight units in the first category (one to three birds), and the relatively minor differences between larger corresponding categories. The morning and evening flights have been divided approximately in half numerically in computing the "first portion" and "second portion" shown in these graphs.

Just why there should be a tendency for flocks to be larger near darkness I do not know. Perhaps it results partly from the fact that more birds are flying at those times, so there are more opportunities for them to join. But I cannot believe this is the complete answer; since, in both the morning and evening flights, the periods when the greatest

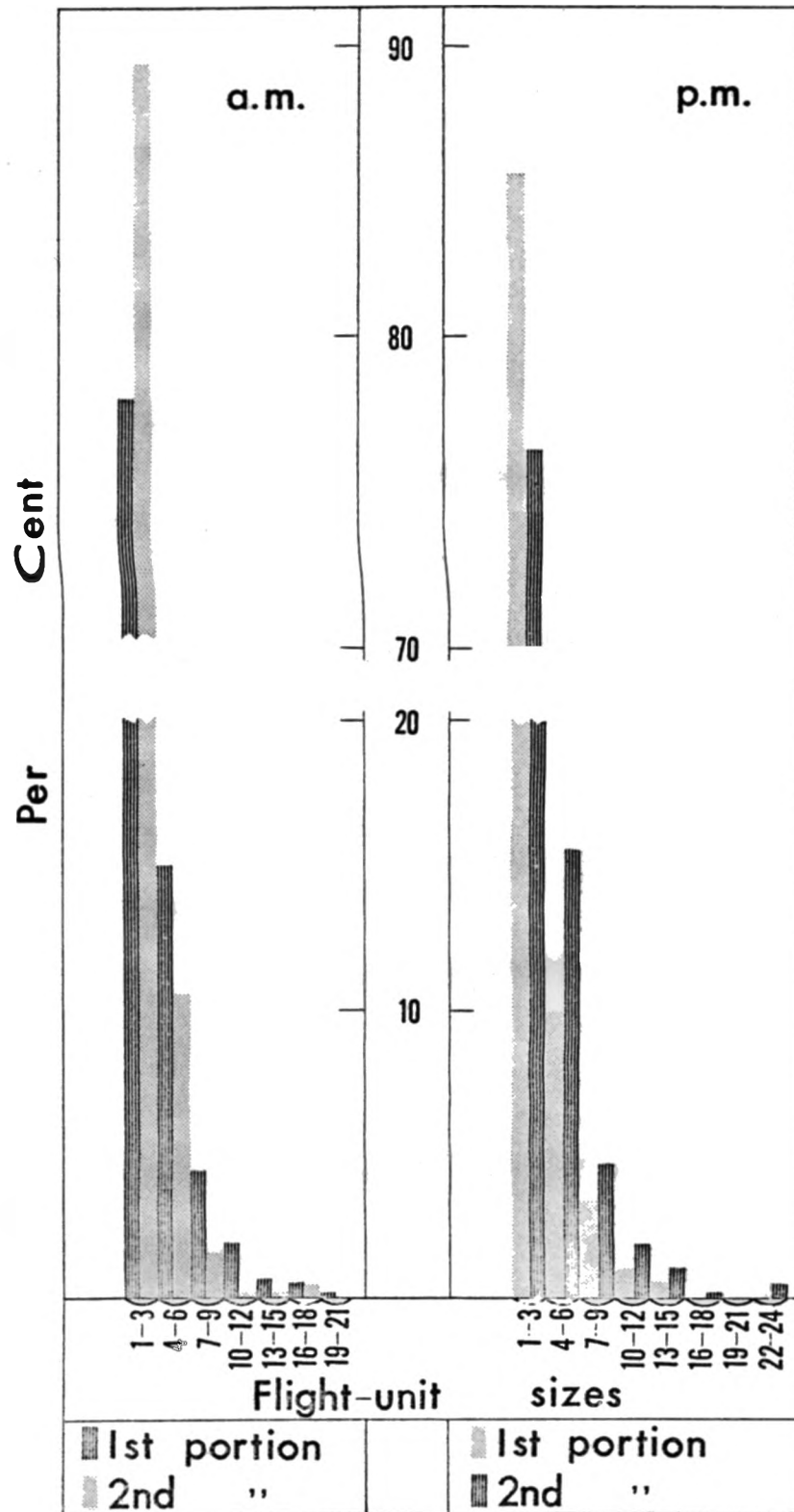


Figure 5. Per cents of various sized flight units in total flight composition of the first and second portions of morning and evening flights.

numbers of birds were counted were not the periods of greatest average flight unit size. Another factor may be the need for the birds to help guide one another after dark.

The boobies' morning flight to their fishing grounds always began well before daylight and reached a peak thirty to forty-five minutes after daylight. Just how early the flights began is unknown. The lighthouse keepers frequently told me of seeing boobies flying in the light beams at all hours of the night. And I have seen them by moonlight, fully half an hour before daylight, flying out in considerable numbers. According to Sharpe (1904), they continue fishing all night during moonlit periods, and from my experience I believe this is true. In fact, they may feed or fly about to a limited extent even throughout moonless nights. I often checked the colony late at night to find that birds were gone from roosts where they had been earlier that evening.

Departure flights differed from day to day depending on the direction and force of the wind. Prevailing winds at Half Moon Cay come from an easterly direction, and under those conditions flight units departed from a center of soaring birds above the south point---Figure 6a. The centers of soaring birds were characteristic of the morning flights when there was ample wind to permit soaring. And invariably Magnificent Frigate-birds (Fregata magnificens) formed a prominent part of the soaring group. The boobies left their nests and flew eastward until they were above the south point. There they soared among the other

boobies and the frigate-birds before heading out alone or with other birds toward the east. Normally the birds stayed about 100 feet above the water until just at the reef's edge. There they dropped down near the surface and continued eastward, apparently already on the alert for any flying fish that might dart out ahead of them. Occasionally, however, the birds remained at about 100 feet until well out of sight to the east. The number of soaring birds in the flight unit formation center seldom became large; however, one morning I saw as many as sixty boobies soaring over the point at the same time. This was during a strong east wind, which made it easy---and perhaps enjoyable---for the birds to soar. During east winds, nearly all the birds passed to the south of the lighthouse, but the more the wind shifted to the north, the greater was their tendency to pass eastward to the north of the lighthouse.

When the wind shifted well around to the north, the flight units formed over the center of the western, and largest, half of the cay (Fig. 6b). This put the group formation center more nearly above the birds' nests, so they could no longer fly directly to the formation area. Instead they had to gain altitude by spiraling or zig-zagging upward toward the soaring birds. Flights leaving from that formation center headed either northeasterly and then easterly to pass north of the lighthouse or due east over the cay itself and out over the water just south of the lighthouse. During northwest winds the flight units formed directly over the northwest end of Half Moon Cay and veered back over the full length of the island to pass, again, just south of the lighthouse (Fig. 6c).

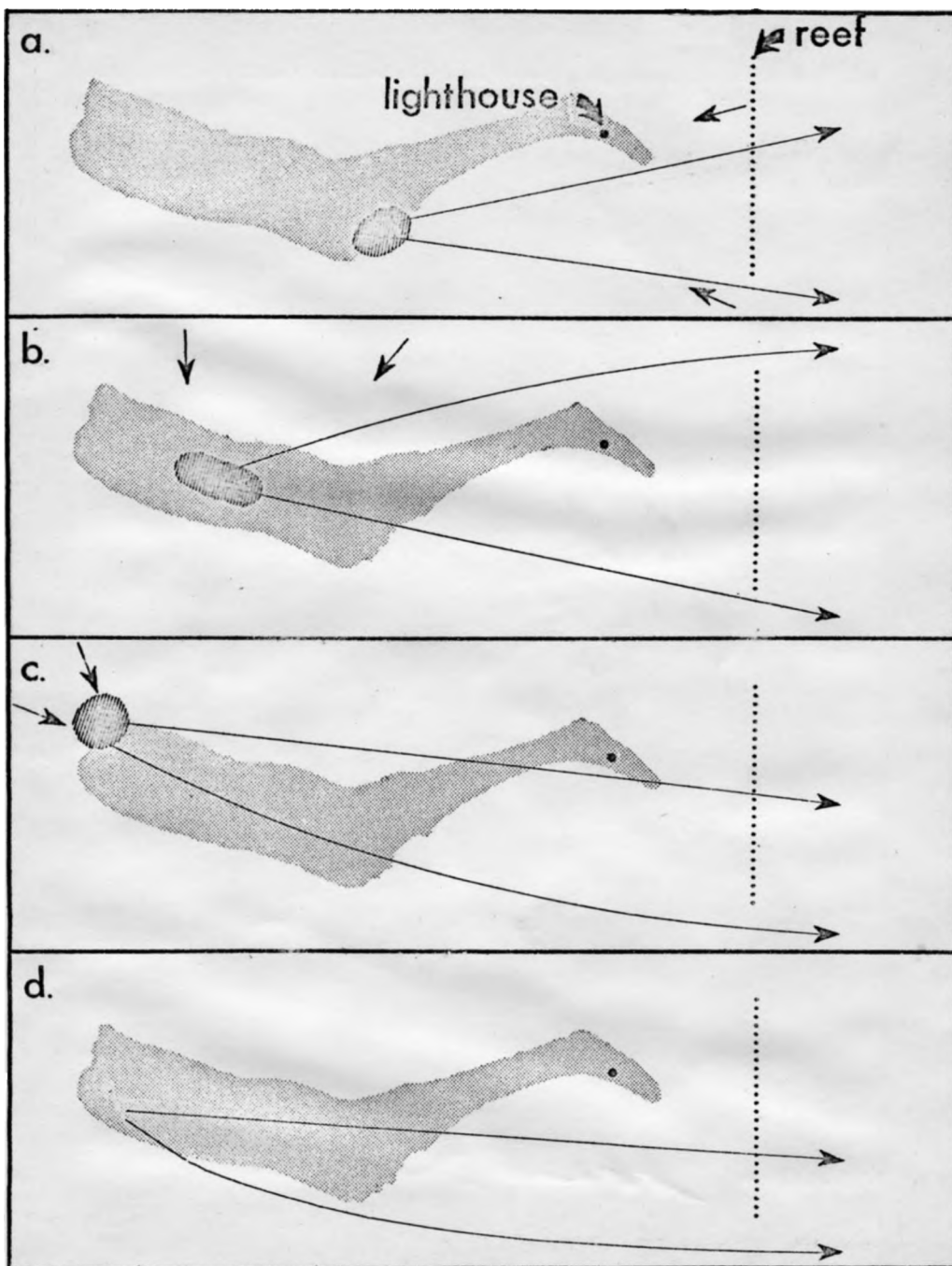


Figure 6. Flight unit formation centers (darkly shaded) and principal direction of flight departure (long arrows) as influenced by wind direction (short arrows). Note (d.) that when there is no wind there is no unit formation center.

And finally, when there was no wind or only very light wind, there was no soaring center from which birds departed to the east. Instead they left directly from the colony, usually paralleling the southern shore, and began flying just above the water well before reaching the edge of the reef. Or they flew eastward from their nests just above the tree tops and dropped near the water's surface opposite the eastern shore of the south point (Fig. 6d). This last departure pattern occurred at all times but was prevalent only under calm conditions. Notice that, although wind direction determined the location of flight unit formation, it had no effect on the final direction of flight. The vast majority of boobies headed east from the cay in spite of the wind. Regularly, however, scattered individuals flew to the south, and on rare occasions a few flew to the north. Every such bird that I followed with my binoculars eventually swung around and headed east before I lost sight of it. I never once saw a booby depart to the west.

During midday, that is between the drop-off in the morning flight and the onset of the evening flight, there were relatively few Red-footed Boobies flying to or from the cay. Average flight unit size dropped to 1.46 and there was never an area of soaring birds from which flocks departed regularly. Birds could ordinarily be seen flying out all morning. In fact I rarely had to wait longer than five minutes to see one or two birds fly eastward. Returning birds were observed infrequently in the morning and more frequently during early afternoon.

The evening return flights began slowly, increasing about one and three-quarters to two hours before dark. The peak periods occurred between fifteen and thirty minutes before dark (Fig. 3) except on the evening of February 20. On that evening there were two distinct "peak" periods, with the first slightly larger than the second. The first peak occurred fully an hour before the normal time, and I am at a loss to explain it on any basis other than chance variation. That on some evenings a great number of birds may remain at sea very late and so return after dark or not at all is convincingly demonstrated by the morning and evening counts of April 19. On that morning 1062 birds were counted flying out, but only 756 were counted returning that evening. Undoubtedly many birds left in the morning before daylight so were not counted; therefore well over 300 birds remained unaccounted for by dark that night. Perhaps some of them did remain at sea during the night, but probably most returned to their roosts after dark.

Most of the birds returned to the cay in the evening from points between northeast and south. A few returned from the north or the southwest, but I never saw any return from the west. However, birds returning from the southwest reached the island at its western tip; so, from points of observation within the colony where the birds could not be seen approaching over the water from the southwest, they appeared to be returning to their nests from the west. Early flocks usually approached very high; I estimated their elevations at fully a half mile. The high flights ordinarily remained together until nearly above the

nesting area. Then they broke up, and each bird glided down in a wide spiral on half-closed wings. Normally the full descent was made in less than two complete circles, and frequently a bird interrupted its spiral to dive nearly straight down with its wings nearly closed and its webbed feet spread widely and extended below it. When just over the tree tops, it took the shortest route to its nest.

One of the least variable features of a bird's return to its territory was a raucous, rattling series of guttural squawks begun just before landing and ended shortly after. This I called the "landing call," and it was the most characteristic sound of the colony. The call, uttered at the rate of four to seven notes per second, was also used at times during threat displays. The birds usually craned their necks about as they squawked after landing, an action also noted by Gifford (1913) among the Red-footed Boobies at Cocos Island in the eastern Pacific. The call was common to both sexes, and silent landings were such rare occurrences that I usually recorded them.

Not every bird returned at such a high elevation. A great number came in at levels between 100 and 500 feet; and, as darkness approached, more and more seemed to be at these lower levels. The lower flocks tended to break up when as far as a mile from the colony and seldom kept order as a flock when within a half mile of it. The birds hurried at such times and, with a tail wind, frequently sailed in without a single flap of wings from more than half a mile out. The returning flight of the boobies, with the flocks of white birds against the reddened sky, is one of the most beautiful and relaxing parades I have ever watched!

NESTING BEHAVIOR

Nesting Season.

When I arrived at Half Moon Cay, I found that there were wide differences among the pairs in respect to how far they had progressed in their nesting activities. Some pairs were still building while others had young well advanced. This pattern seems to be the rule in colonies of this species throughout its range, and the most striking example was cited by Richardson (1957). At French Frigate Shoal, in the Hawaiian Archipelago, he found only two trees occupied by Sula sula. A photograph of one of the trees showing six nests shows a range in laying time of "at least three and a half months!" By calculating back from the date I observed the first flying young (April 1), I have fixed the earliest date of laying at Half Moon Cay at about November 15. Courtship and nest building would extend the nesting season backward at least another two weeks. Gilbert Saunders continued checking 11 nests for me until September 18, and there were still flying young returning to their nest sites at that time. Thus the nesting cycle for the whole colony at Half Moon Cay runs for about 11 months. The cycle for each pair lasts at least six months.

Territory and Pair-bond.

The Red-footed Booby, being the only species in its family

regularly nesting in trees (except Sula abbotti in the southwest Indian Ocean), naturally has a different sort of territory from that of the familiar boobies and gannets. The territory of the Red-footed Booby is used for nesting, copulation, and occasionally for roosting by the nonincubating mate. Usually, however, the nonincubating bird roosts on a perch, which is often shared with other birds and is removed from all territories. Each territory, therefore, is small, including only the nest and three or four nearby perches used for landing and take-off. Most territories probably do not exceed six square feet, but I was aware of a possible exception. One of the pairs I was observing closely from day to day had a take-off perch fully ten feet from its nest, apparently because the shrub holding their nest did not provide a suitable perch for take-off. The perch was defended only when the birds wanted to use it themselves, and the same perch was used by at least two other pairs that always yielded to the first. Strictly speaking, this perch was common ground to all three pairs; but, since there was a definite dominance of it on the part of the one pair, it might be considered as a part of their territory removed from the nest territory.

Territorial defense was, at times, quite fierce. Adults and moderate-sized young alike were active in defending the territory against all intruders, including strange boobies, frigate-birds, Wish-willies, Iguanas, and men. Although the degree of resistance to me varied considerably among the individuals, nearly every adult booby stood its ground at the nest until I removed it bodily. I was always armed with a

forked stick two feet long that I worked under the sitting bird until it was forced to stand on the end of the stick. Then I raised it into the air with a swing of the stick and sent it flying on its way. The first few times I disturbed them, the birds were very active in resisting me, biting and stabbing at my hand and the stick and squawking loudly. But gradually they became accustomed to my intrusions and only tried to bite me, paying little attention to the stick and not squawking. They reacted similarly to a mirror on a long pole that I used to examine the contents of nests high in the trees. The adults would not attack strange downy young if I moved one from another nest, but nestlings fiercely resisted intrusion by other young. Smaller young on their own nest invariably whipped larger young introduced from other nests. The birds fought with their bills, biting and jabbing each other until one or the other withdrew. Several fights looked like struggles to-the-death.

One evening I saw a bird (A) land on the territory of another (B). B immediately jabbed A with its bill and drove A back about two feet to another perch. B held ground and A retaliated. They "one-pointed" (threat display described later) at each other for several seconds, both with the typical shrieking squawks and head waving. Suddenly B gripped A's bill and pulled A from its perch. Momentarily A hung in B's grip, trying to get a foothold on some branches. Finally B released its hold on A's bill, and A began clambering back up to its perch. B jabbed A in the middle of the back; A slipped; and B jerked A's tail. Then A lost all footing and dropped at least ten feet to land in a heap beside a large downy

young in a nest below. The entire encounter lasted but a few seconds and was certainly one of the most violent, and yet comical, I observed. On other occasions I saw one bird grip another by the neck and hold so tightly the victim was unable to free itself. As a rule, however, territorial defense did not involve physical contact; simple threat displays were enough to keep intruders out.

I called the principal threat display the "one point." Both sexes gave this display, but the males were generally more aggressive. In a typical, exaggerated one-point, a booby thrust its bill forward toward the intruder and waved its head slowly and methodically from side to side. Usually, though not invariably, this action was accompanied by a series of loud squawks, normally with a screeching quality. Ordinarily the threat was given from a sitting position by an incubating bird, although the birds also one-pointed while perched. In its mildest form, the one-point involved only the forward thrust of the bill without the head-waving or calling, and all gradations between the two extremes were observed.

A second display, named the "stick-wave," was used to denote territorial ownership; in most cases where the sex was known, this display was performed by males. The displaying bird, standing on a perch with a stick in its bill, waved its head about while holding the stick and uttering a series of guttural squawks indistinguishable, or practically so, from the call given by all boobies when landing. This action was performed most often by males returning to their territory with a twig for the female to add to the nest. However, on several occasions, I observed

immature birds that had nearly attained the adult plumage giving the stick-wave. One such bird occasionally gave the display, always from the same perch, for a period of at least two months. It not only waved the stick about and squawked loudly but also made several motions as though to place the stick on its perch. The bird was present at its perch every evening, and frequently it engaged in lively battles with nesting adults whose territories were nearby. In several cases it appeared that the immature was deliberately challenging the other birds to dispute his right to that spot. To me these antics were suggestive of territorial selection.

A third display that seemed to be used to proclaim territory and to warn intruders away I called the "four-point." This display, however, was primarily used in intersexual ritual and will be described in detail later on.

On the basis of indirect evidence, I suspect that the male selects the territory. The male of a nestless pair that was maintaining a territory was killed; and, since the female was marked, I was able to trace her movements after the male was gone. In two days she had deserted the territory and in the evenings was roosting near my observation platform. The female of another nestless pair that had been maintaining a territory for at least a month was killed. The following day the male was not seen, but the day after that he was back on his territory. Three days after his first mate was killed, that male had a new mate! The pair remained on the original territory but never attempted to build a nest.

I mentioned that these were nestless pairs. Several such pairs were observed closely for long periods of time. From those observations I could not help feeling that perhaps at least some pairs maintain their territories throughout the year. And more likely still is the possibility that the monogamous pairing of this species is at least sustained, if not life-long.

One pair was numbered on February 21. Their nest was empty on that date, and on March 4, it was gone. I had been examining the nest twice daily in an attempt to establish a laying date, and apparently my disturbances caused the birds to desert their nest long enough for other boobies and the frigate-birds to remove it. Nevertheless, this pair maintained and vigorously defended their territory throughout my stay at Half Moon Cay. During the entire three month period, they made no serious attempt to reneest; though occasionally they performed a ritual with a stick that will be described later. Their actions were typical of the nestless pairs I observed, although I suspect that at least some of them established new territories after the loss of their first nests.

Unlike nesting pairs, both birds of the nestless pairs were absent from their territory most of the day. In the evening they invariably returned separately; so the probability is that they were not together while fishing. Their evening antics assumed different forms, with each pair tending to emphasize one or another feature of the general pattern of activity. For example, Pair 64 stressed the four-point and "stick-shake" displays; Pair 70 usually sat quietly while the female preened the nape

and back feathers of the male; and Pair 75 concentrated on the four-point and actual copulation. That was the only nestless pair I noted copulating, although Pair 74 made several unsuccessful attempts to do so. It seems especially unusual in the case of Pair 75 that, although they copulated regularly for a full month, they never attempted to build a nest. An examination of Female 75's ovary revealed no enlarged follicle, and the significance of their activity remains a mystery. The other activities mentioned were common to all pairs, and I feel confident that both the four-point and the stick-shake are important in pair-bond formation and its maintenance.

The four-point and its variations were probably the most frequently observed displays. I named this pose the four-point because, in its most exaggerated form, the bill, tail, and both wing tips were directed skyward as illustrated in Figure 7C. The posture was accompanied by a single rattling, drawn-out note usually on a low pitch and with only a slight inflection at the end, or none at all. I phoneticized the sound variously in my field records, but probably "walk," or better "waaalk," fits the note best. The posture began with the booby extending its head and bill upward until the bill was nearly vertical, thus exposing the throat area (Fig. 7A). Before this action was completed, the tail began to rise toward a vertical position (Fig. 7B), and the wing tips were directed upward before the head and tail were fully erected. The wings were not extended from the body, however; instead the elbows were depressed with the forewing and manus directed upward and the remiges spread. All the

actions were slow and deliberate, and the full posture, as just described, was not always attained. Rarely a four-pointing bird that was standing on a perch terminated the display by bowing very low (Fig. 7D). Every gradation between the full pose and simply raising the head and bill slightly was observed, and it was impossible to distinguish between a beginning four-point pose and a weak one-point.

The four-point was primarily a display of the male; although occasionally mated females without nests and more rarely immatures were seen in the posture. The posture was used most in intersexual rituals between mated birds, but sometimes it served as a threat or to denote territorial ownership. In the latter cases the display rarely assumed exaggerated form and often was performed without the call. The partners of nestless pairs were noted on several occasions four-pointing to each other nearly in unison. Normally, however, the male was the more active partner, and the female responded to the display simply by bowing or thrusting her bill toward the male or showed no visible reaction whatever. Males of nestless pairs were certainly more active in their displaying than males assisting with nesting duties; so it was from the nestless pairs that I obtained my best series of observations.

I consider the following a typical example of the complete, formal four-point display involving both members of a nestless pair. The complete ritual was never noted among the nesting birds. The male was standing on a perch facing his mate, who was standing on another perch

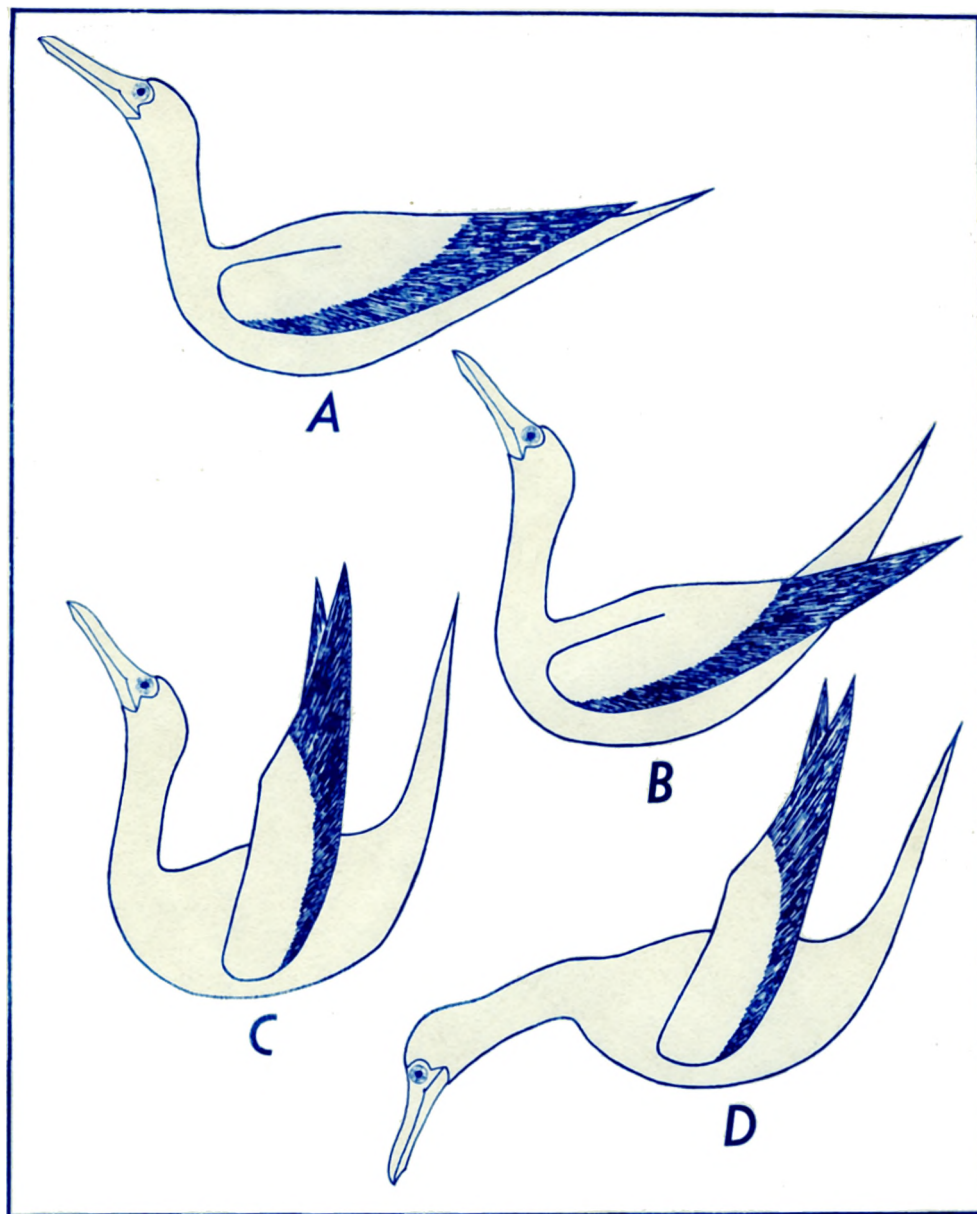


Figure 7. Stages of the four-point display. A, B, and C illustrate typical stages in the display with C being the usual climax position. D illustrates the "bow," which infrequently followed stage C.

about two feet away. The female seemed to be paying little attention to the male; but he was intent on her, never moving his gaze from her. He tried to command her attention by extending his neck fully to thrust his bill in her direction. If she turned toward him, he began a four-point. But if she turned away before he reached the full pose, he relaxed and again thrust for her attention. Only when the female gave the male her full attention did he give the full four-point and thus expose his colorful chin and throat to her. I never saw any bird expand, or in any way enlarge, its gular sac during any display. The female frequently acknowledged the male's display with a bow or bill thrust in his direction, and occasionally she assumed a four-point herself. However the female rarely went into the full posture. During one such ritual a female was initiating every four-point, and the male was responding with the same, so that both reached the full pose at nearly the same instant.

Although this display was used, especially in its incomplete stages, as a warning to trespassers, I feel confident that its chief importance is in courtship and maintenance of the pair-bond. Since nesting males four-pointed only occasionally, it is probable that their domestic responsibilities are sufficient to maintain their pair-bond. The stick-shake display was observed more among the nesting pairs than the nestless pairs, so perhaps it helps to serve the function four-pointing serves during the nestless period.

The stick-shake, as its name implies, is a ritual centered around

a stick. It was observed frequently among the nesting pairs but not often among the nestless ones. Without exception, the male of a pair of nesting birds gathered the nest materials after construction was begun; and materials were added to the nest even throughout incubation and during at least the first two or three weeks of the nestling period. Each stick was brought to the nest with a great deal of squawking and usually much head waving---this activity is identical to the stick-wave display. After the male finished the stick-wave, he passed the stick to the female for her to make the placement and adjustment on the nest. Frequently, however, both birds held the stick and shook it mildly. Then they arched their necks forward and down together to place the stick on the rim of the nest. Without exception, when either sex or both together held the stick down at foot level to place it on their nest or perch, it was trembled or quivered into place. The stick often became quite a toy for the birds as they passed it back and forth between them. The male normally waved his head about with the stick in his bill and squawked loudly in a call like the landing call; the female, when she had the stick, usually placed it here and there on the rim of the nest with no accompanying notes. Apparently at such times the stick-wave display merges with the stick-shake display. It remains a question whether or not the stick-wave serves the same function when performed with the stick-shake as it does when performed separately; however, I suspect that it does. Unlike nesting pairs, both sexes of the nestless pairs gathered the sticks, but the antics between birds were the same after

the stick was secured. It was finally dropped to the ground by those birds, however, since they had no nest to which to add the stick.

Since only the males of nesting pairs, and both males and females of nestless pairs, were observed gathering nest materials, and since the females of the nestless pairs were invariably the first noted and the most active at gathering materials, I suspect that female Red-footed Boobies initiate nest construction when they are ready. The males then assume the gathering responsibilities entirely, while the females carry on most of the actual construction. This difference in activities between sexes of nesting pairs was very useful in distinguishing sexes after the male's facial colors had reverted to the nonbreeding condition, and he again appeared similar to the female.

The Nest.

The Red-footed Boobies on Half Moon Cay utilized eight species of trees as nesting cover (Table 4). The highest nest in the colony was 35-1/2 feet above the ground; the lowest was 8-1/2 feet; and the average height of 100 randomly selected nests was 18.4 feet. Holt (field notes, 1926) wrote that nests at Half Moon Cay were from "no higher up than 5 ft." to some "that must have been 35 ft. from the ground." I found no record of higher nests in any part of the world; apparently the nest height depends primarily on the height of available vegetation. Nests as low as one foot above the ground were recorded at Willis Island, Australia (Reithmüller, 1931), Raine Islet, Australia

SPECIES	TOTAL NESTS	TOTAL TREES	AVE. NO. NESTS/TREE
<u>Cordia sebestena</u> ----	783 -----	363 -----	2.16
<u>Bursera simaruba</u> ----	232 -----	77 -----	3.01
<u>Bumelia retusa</u> -----	210 -----	130 -----	1.62
<u>Pouteria campechiana</u> -	86 -----	45 -----	1.91
<u>Ficus</u> sp. -----	50 -----	25 -----	2.00
<u>Ximenia americana</u> ----	22 -----	7 -----	3.14
<u>Pithecellobium keyense</u> -	4 -----	2 -----	2.00
<u>Neea choriophylla</u> ----	2 -----	2 -----	1.00
Total -----	1389 -----	651 -----	2.12

Table 4. Species of trees utilized as nesting cover by Sula sula at Half Moon Cay, with a breakdown of the number of nests in each species.

(Macgillivray, 1918), and Trinidad Island (Wilson, 1904). Vesey-Fitzgerald (1941) recorded nests from three to twenty feet up at South Island of the Farquhars, Indian Ocean; and Snodgrass and Heller (1903) recorded nests four to five feet up at Tower Island in the Galapagos. Finally, Ridgway (1895) estimated nests at fifteen to twenty feet up at Glorioso Island, Indian Ocean.

Ground nesting of this species is, indeed, a rare occurrence. On San Benedicto Island, in the Revilla Gigedo group, Sula sula websteri nests on grass culms from one to two feet high (Anthony, 1898; Beck, 1902; Kaeding, 1905; Hanna, 1926; and McLellan, 1926). The island is bare of trees, but still the birds choose to nest there. At Jarvis Island, Kirby (1925) has photographed Sula sula rubripes nesting on piles of sticks a foot or more high. And Hutchinson (1950) wrote that Hague mentions a booby with that habit on Howland, presumably Sula sula. These are the only ground-nesting colonies of this species I know of in the world, and I have records of at least 72 separate nesting colonies. In each case the birds have improvised platforms to elevate their nests at least a foot; so, still, they do not nest flat on the ground.

At Half Moon Cay most nests were placed near the tops of the trees or on their outer edges where the birds could utilize winds or drop from their perches when taking flight. They were situated on top of criss-crossing networks of small branches that provided suitable platforms; in the angles of wide, flat crotches; or on top of nearly level limbs. Describing the nest of Sula sula rubripes at Moku Manu, Hawaii,

Richardson and Fisher (1950) write; "The booby nests when first built consist of a handful of fresh branches, as of Atriplex, a foot or two long, bent or placed in a rough circle on top of a low bush. The booby packs these branches down, adds more branches, and bends the living bush down with its weight so that a rather flat, nesting platform results."

Murphy (1952) remarks that the Red-footed Booby at El Fondeadero, Hermanos group, nests in trees and shrubs on the windward slope to have a good windward take-off. The largest area without nests in the colony at Half Moon Cay, shown in the center of the nests plotted in Figure 8, was in a vegetational pocket. I feel certain the chief reason no birds nested there was because there was not enough wind in the pocket to aid them in taking flight.

Figure 8 is a plotting of 95 nests in a 0.83 acre tract around my observation platform; every nest included within the area is accounted for on the map. The plot had a nest density of 114.5 nests per acre; nest density in my main study area (3.99 acres) was 131.8 nests per acre; in the remainder of the colony (6.97 acres) the density was only 123.8 nests per acre; and the colony as a whole had a density of 126.7 nests per acre. These figures, however, have little value in determining average territorial size; since a great percentage of the area had no nests. The nearest two nests in the plot were only nineteen inches apart.

Nest materials were gathered by the males, at least after nest construction was seriously underway (see discussion under Territory

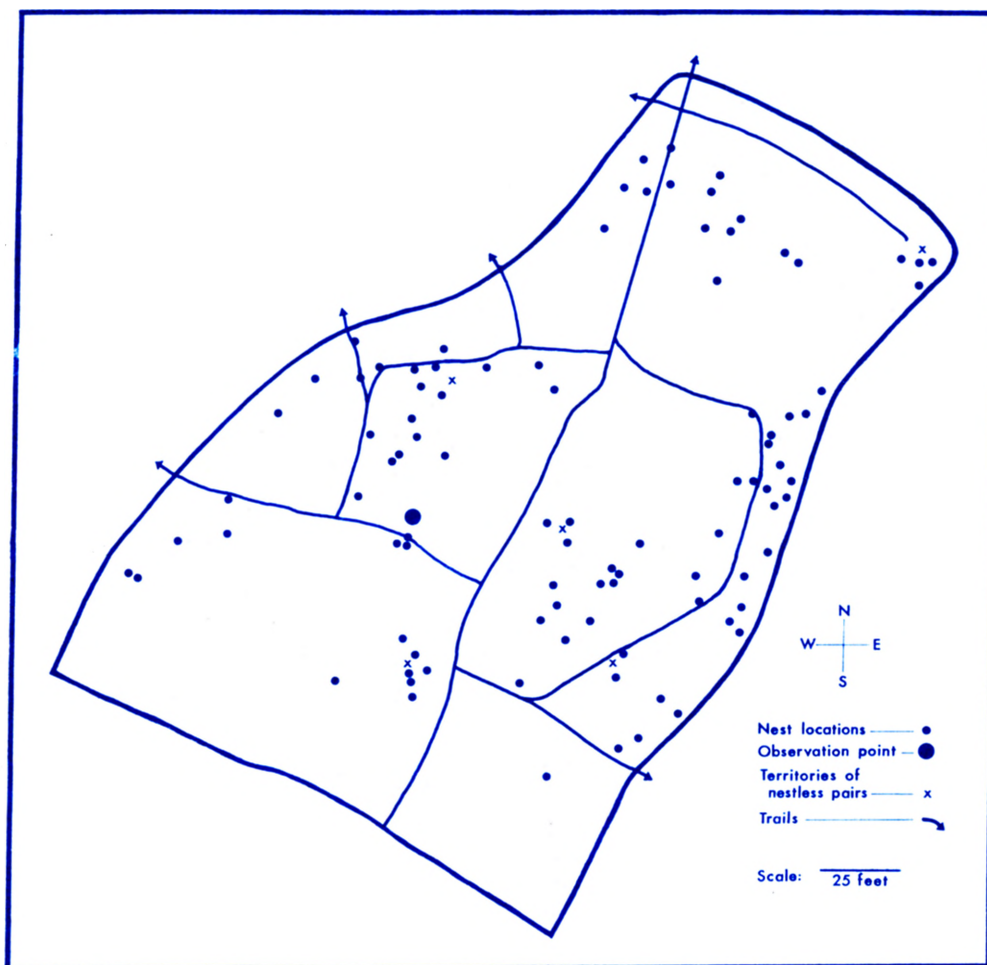


Figure 8. Plotting of nest locations on a 0.83 acre area around my observation platform. The southwest border marks the tree margin; the beach extends beyond. Notice that none of the nests were placed near the edge of the area toward the beach; this was typical of the entire colony.

and Pair-bond). The females sat at the nest site and placed all the materials brought by their mates. Stealing of nest materials was common among the boobies, and nests that were vacated when other pairs were still adding to their nests were quickly dismantled and carried off by other birds. Twigs and small sticks were broken from the trees; and, on very windy days during the height of the construction period, the birds pulled up coarse herbs from the ground on the windward shore. In fact the males concentrated all their gathering activities on the windward side of the cay. Mr. George Young told me that he has seen a number of boobies practically strip a small bush to the trunk before leaving it to gather sticks elsewhere. The result has been a curious hedgelike shearing of the trees along the southern and eastern borders of the nesting colony, facing the direction of the prevailing winds. At first I thought this was the result of wind-sand abrasion, but the tips of all the twigs had been snapped off; innumerable pockets had been broken out; and, finally, neighboring cays exhibited no such trimming of shoreward vegetation. The frigate-birds and Ospreys (Pandion haliaetus) may have contributed to the shearing.

The nests were composed of small sticks, twigs, and coarse herb stems plucked with the leaves still attached. As a result, the nests frequently had streamers of sticks bearing dry leaves hanging down from their rims as far as 500 mm. Of the 27 nests I measured (the total number I could reach with my ladder), 24 were circular and three were

slightly oval. The diameters of the circular nests ranged from 260 to 420 mm. and averaged 306 mm. The dimensions, in millimeters, of the three oval nests were 480 X 340, 340 X 190, and 380 X 300. The depths of all the nests---top of rim to bottom of compacted portion of nest body and not including leaf streamers if such were present---ranged from 75 to 180 mm. and averaged 113 mm. Nest depressions were very shallow, rarely an inch deep; and nests became progressively more flattened after the egg hatched. Two abandoned nests were collected and examined. One contained 162 separate sticks and herb stems between 2 and 8.5 mm. in diameter and from 77 to 689 mm. in length. The other consisted of 156 sticks and herb stems from 1 to 10 mm. in diameter and from 51 to 638 mm. in length. The latter nest also included 82 gms. of dry leaves. The herb stems comprised a very small percentage of the total nest bulk in each case. Excrement was a part of all nests, but I do not believe it was ever consciously incorporated into the nest by the adults.

The only nest of which I observed the complete construction was a second attempt by Pair 22, which had their territory just twenty feet in front of my observation platform. These birds lost their first egg on February 15, but they clung to their original territory after the loss. However, they both left the territory during midday, and neighboring boobies and frigate-birds took all the material from their nest. This common practice in the booby colony dictated that at least one member of a pair be on guard at all times to protect the nest even before the egg

was laid. I saw nests completely stripped and added piece by piece to other nests in thirty minutes! On March 4, Pair 22 had definitely begun to build a new nest in the same position as their first. At 5:47 p.m. they copulated at the nest site; then the male flew off while the female guarded the new nest, which consisted of a very few sticks at that time. At 6:03 p.m. the male returned with a twig bearing dying leaves that was probably taken from a nest recently deserted by another pair.

The male guarded their nest all the following day. At 4:22 p.m. his mate returned, and the two birds immediately began adjusting nest materials. Between 4:27 and 5:57 p.m. ---a period of just one and a half hours---the male brought 41 separate sticks for the female to add to their nest. The first 39 were taken from a vacant nest just eleven feet away; the fortieth was obviously freshly broken from a tree and was covered with fresh leaves; and the last was apparently taken from a vacated nest out of my sight. Each time the male returned to the nest with a stick he squawked loudly just before alighting. After landing, he frequently craned his neck, waved his head about, and squawked with the stick in his bill (stick-wave display) for a few seconds. Occasionally the female responded with a soft, squawking chatter. She invariably made the final placement of each stick on the nest; although the male often helped her move the stick toward the nest, both birds holding it together. All the sticks collected that day were added to the rim of the nest, with the female working all of them in about her and

occasionally turning around and around in the bottom of the nest.

Without fail each stick was quivered or trembled into place. Just before dark the birds copulated and then settled down to roost.

For the next few days one or the other of the birds guarded their nest, and construction continued more slowly. At 11:12 a.m. on March 12, just eight days after their nest was begun and 25 days after the loss of their first egg, Female 22 laid another egg. The birds continued to add to their nest occasionally throughout incubation and even after the young was hatched. Other pairs were also observed adding to their nests after they had young, in fact one male was seen collecting nest materials a month after the egg had hatched. It was not, however, a common practice for the boobies to do so, and I suspect that the case in which the pair was adding to a nest containing a month-old young was an extreme one. Twigs freshly broken and bearing fresh leaves were added to the lining of the nest before the egg was laid and throughout incubation, and dry leaves were occasionally removed from the lining. Fisher (1903) wrote that at Laysan Island he found leaves scattered under the eggs in newer nests. He used these leaves as a rude index to the incubation stage of an egg, assuming that the drier they were the longer the egg had been incubated. However, since fresh leaves were added to the nest lining throughout incubation at Half Moon Cay, I am rather skeptical of this sort of index!

Below the nests at Christmas Island, in the mid Pacific, Streets (1877) noted mounds of twigs one or two feet high, sometimes cemented

together with excrement. "It probably afforded them diversion during the monotonous period of incubation to break off all the twigs within reach of their bill, and to drop them under their nests. These mounds furnish evidence of the nests being occupied for several successive years; for the lean bushes could not furnish a sufficient amount of twigs to build them up in a single breeding-season." The evidence presented is certainly interesting and unique; I found no such record for any other colony of Red-footed Boobies anywhere. If, indeed, the birds at Christmas Island do use their nests for several successive seasons, it lends support to my beliefs that at least some pairs maintain territories all year long and that the pair-bond is sustained or life-long. At Half Moon Cay I doubt that many nests could survive the stormy season. Even by the end of my stay a few of the recently abandoned nests had nearly collapsed. As an additional factor against the use of nests in successive seasons, the young birds usually left their nests to stand on perches long before fledging and, from there, tore their nests apart, piece by piece, until nothing was left of them.

Young boobies became progressively more active and restless as they aged and eventually began scrambling out on the various perches of their territories. However, they rarely ventured more than a few feet from their nests. When I first saw perching "nestlings" with no nests nearby, I wondered if neighboring adults had stolen the nest materials after the young moved off. That seemed unlikely, however; since even young boobies viciously defended their territories against intruding

adults. It was not until the evening of April 11 that I realized what had actually happened to the nests of the perching young. On that evening I watched a young bird actively dismantling his nest. In seventeen minutes he removed sixteen separate sticks and several leaves. The young actually played "catch" with each piece he secured, tossing it an inch or two into the air and catching it again in his bill until he missed the catch and dropped the stick. Each time he tore another stick from the nest, several others were loosened and tumbled to the ground. By the time he was finished, only a few sticks of the nest remained, and the following evening those were gotten rid of too. Ordinarily the young tore their nests apart three or four weeks before they were ready to fly, but some did so even earlier. Eighty-one of the 221 nests I checked weekly during my three-month stay on Half Moon Cay had flying young when I left, and 74 per cent of those 81 young had removed their nests.

Copulation.

Copulation occurs at the territory, either on the nest or on a perch, but I am nearly sure it never occurs at sea. After nest construction begins, one member of a pair must be at the territory at all times to guard the nest materials against theft by other birds. Since the birds are rarely together at the territory during midday, copulation must necessarily take place either in the early morning or late evening. My observations indicate that it occurs most frequently in the evening, occasionally in the early morning, and rarely during midday. Copulation by nestless pairs has already been discussed.

Little or no preliminary ceremony preceded copulation. Usually it took place during periods when the male was gathering materials for the nest. Occasionally, he alit directly on the female's back when he returned with a stick, the stick was passed to the female, she placed it on the nest, and copulation followed. More often, the male alit beside the female; a stick-shake display followed, or the female placed the stick directly; and the male mounted. Just as the male mounted, he gave a loud, guttural, drawn-out screech. The female frequently raised one wing slightly, which served to lend support to the male. He put his bill beside her neck, frequently shifting it from one side of her neck to the other but never taking her nape feathers in his bill. Then he slid backward over either her left or right side, sometimes flicking his tail from side to side just before cloacal contact. After the initial screech at mounting, the male began a series of low, guttural notes given at a rate of about 1 to 1-1/2 per second. Like the note accompanying the four-point, this latter note of copulation is best phoneticized as "walk." But, unlike the four-point call, the copulatory note has a pronounced inflection in the middle. The series of notes continued until just after cloacal contact was effected and the male had again assumed a standing position on the female's back. He remained standing there for various periods of time up to two minutes before hopping to a perch or flying off.

I never heard the female make a sound during copulation. However, on a very few occasions, I saw the female mount the male and remain a short time without attempting copulation. During those times

the female gave part of the typical copulatory call of the male, and once one gave the full sequence of notes. Only nestless females were noted in this activity.

Pair 22 was noted copulating eight days before the female laid. I observed them copulating once each evening on the eighth, seventh, fifth, and fourth days before the egg appeared. The day before Female 22 laid, she remained on the nest all day, and Male 22 stayed in the colony gathering nest materials most of the day; I observed the pair from 5:30 a.m. through 6:30 p.m. I heard copulatory notes as I climbed to the observation platform at 5:30 a.m., and Male 22 was standing on his mate's back when I got within view of the birds. I feel sure that they copulated. They copulated at 7:10 a.m., 9:57 a.m., 11:06 a.m., 1:36 p.m., 4:02 p.m., and 6:12 p.m. When I left at 6:30 p.m. Female 22 was asleep on the nest with her bill and head tucked back under her scapulars, and Male 22 was standing beside her.

The following morning the pair copulated at 6:32 and 6:53. The male was away from 8:14 a.m. until 4:52 p.m.; and in the meantime Female 22 laid an egg. At 5:22 p.m. and at 5:31 p.m. they copulated again. The next day the male incubated the egg and the female was away until late in the afternoon. At 6:12 p.m. they copulated again. Illness halted my observations for six days; so I do not know how long Pair 22 continued to copulate after the egg was laid. Pair 72, with an egg on their nest, copulated on the evening of March 24. I do not know the day their egg was laid, but it hatched on the morning of May 5. Calculations

from determined incubation periods indicate that the egg may have been laid one and a half to five days before the last copulation was observed, but I doubt that copulation continues past the third day of incubation.

Eggs and Incubation.

Though I personally never found evidence that the Red-footed Booby lays more than a single egg, some published accounts state that two are occasionally laid. Some species of boobies lay two eggs (though it is said that only one of the young birds reaches maturity), and perhaps that has led some observers to attribute the same habit to the Red-footed Booby without evidence. I have been able to find no definite record of two fresh eggs having been collected from the same nest. Belcher and Smooker (1934) reported that nests on Giles Islet, Tobago, held a single egg each, but that "two appears elsewhere [where?] to be the usual clutch." Kirby (1925), writing of Sula sula rubripes on Fanning Island, reported the following: "As has been repeatedly observed [to what observations does he refer?] regarding these birds, two eggs are laid, but only one young comes to maturity." Bent (1922) wrote that two eggs are laid by some individuals of Sula sula, but apparently his statement is based on published accounts and not on personal experience. And, finally, Baker (1929) stated that one or two eggs are laid, but the source of his information is obscure.

To be sure, had I remained on Half Moon Cay only one day, I might be inclined to believe that some Red-footed Boobies lay and

incubate two eggs. The first nest of Sula sula I examined on Half Moon Cay contained two eggs! However, one of the eggs was stained very brown and looked as though it had been incubated for a long time. Eight days later only the more fresh-appearing egg remained in the nest. One other nest was found with two eggs; and in this case too, one appeared fresh and the other well-incubated. Later that nest also contained only the fresher egg. I believe that in those two cases the females laid eggs early in the season that, for some reason, never hatched. Incubation was continued well beyond the normal period, and finally each female laid a second egg. Later the old eggs were discarded. Maynard (1889), in a description and discussion of the Red-footed Booby at Cayman Island, begins writing of the Blue-faced Booby without explaining exactly to what species he is referring. The behavior suggests Sula sula, and I suspect his entire discussion refers to this species. In it he mentions a nest he found that contained one well-incubated egg and one addled egg.

On February 24, an adult standing on the rim of its nest took the brownish, well-incubated egg from the nest into its bill, tossed its head back twice, and then threw the egg to the ground. I examined the remains of the egg on the ground, and it apparently had never begun developing. That was the only occasion I saw such a thing, but it at least suggests that the boobies can realize that an egg is no longer worth incubating.

In addition to the two nests containing two eggs each, 204 nests

containing a single egg each and 311 additional nests containing a single young each were examined. Most accounts of nesting activities of Sula sula emphasize the fact that only a single egg is laid in a nest, and I doubt that Red-footed Boobies anywhere regularly lay two eggs in a clutch. I wonder if records of their doing so might have originated in someone's locating a nest containing one fresh and one old egg, such as was noted by me at Half Moon Cay and by Maynard at Little Cayman Island. Furthermore, I know that one pair is capable of providing food enough to supply two young; so I suspect that, in the event a booby did lay two eggs, there is a fair chance both would hatch and both the young would be raised to maturity.

Joseph Miller, a young fisherman who formerly lived on Half Moon Cay and who visited the island several times during my stay, told me that during the 1956-57 nesting season he took an egg from one nest and placed it beside the egg on another nest. Apparently the eggs were of equal age, because, according to Miller, both hatched, and the adults reared both young. He was very insistent that the account was true. During the latter part of my study period, I succeeded in shifting several young about on various nests until, in the evening of April 17, the two tolerated each other on the same territory. Both seemed to be thriving thereafter, and on the evening of April 24 I saw the adults feed both of them. When I left the cay on May 9 both young birds were still healthy, and one was able to fly. In another case, the male of a pair with a small downy died, and the female very ably provided for the young thereafter.

Thus, there can be little doubt that Red-footed Boobies are capable of raising two young at a time. I leave the door partially open on the question of whether they ever lay two eggs.

Sula sula will relay if its first egg is destroyed; however, what percentage of them do so I do not know. Pair 1 relaid 27 days after the loss of their first egg; Pair 2 relaid 28 days after the loss of their first; and Pair 22 relaid 25 days after their loss. As noted before, Pair 22 deserted their territory enough during the daytime that neighboring boobies removed their nest. However, Pairs 1 and 2 maintained guard on their nests; so they did not need to rebuild for the second nesting attempt. Richardson and Fisher (1950) reported that storms early in 1948 at Moku Manu, Hawaii, "largely destroyed the eggs and young of this species, and renesting was little attempted even by the end of April."

Eggs of the Red-footed Booby vary in shape from very long ovate to short ovate and are covered with a white limy substance that conceals the light blue or bluish-green shell beneath. Most eggs I examined, however, had a variety of scratches through the limy coat. Apparently the material is still soft when the egg is laid, and the adult booby's nails scratch through it to the shell; however, it is not easily marred after the material has hardened. One hundred eggs were weighed and measured, and the results are summarized in Table 5. The measurements compare favorably with published records (Macgillivray, 1918; Gifford, 1913; Bent, 1922; Belcher and Smooker, 1934; and Fisher, 1903). Unfortunately most of the eggs were not fresh, so the weights lose some

EGG MEASUREMENTS

	Length	Width	Weight
Average	59.4	39.8	47.1
Greatest	<u>72.2</u> X 37.6	58.4 X <u>48.7</u>	58.3
Least	<u>53.3</u> X 40.0	61.9 X <u>36.7</u>	35.0

Table 5. Weights (gms.) and measurements (mm.) of eggs of Sula sula, based on 100 eggs taken directly from the nests on Half Moon Cay. One abnormally small egg measured 49.3 X 34.9 and weighed 27.0; it had very little chalky covering, and I doubt that it had a yolk; consequently I have not included it in the table of maximum and minimum measurements, though it was used in determining the averages.

of their significance. Nevertheless, they help to show how much weight loss is incurred by the egg during incubation. The heaviest egg weighed 58.3 gms. (64.0 X 41.5 mm.) and the lightest only 35.0 gms. (53.0 X 37.4 mm.). The latter egg must have been nearly ready to hatch; since two young birds one day old weighed 33.9 and 42.8 gms., and a young four days old weighed 33.1 gms.

Incubation, begun very shortly after laying, required 42-1/2 to 46 days and averaged 44-1/2 days in the twelve cases I was able to trace. It seems unusual that incubation should take so long; since the egg is no larger than a chicken's, and the young booby is hatched quite naked and helpless. The length of the incubation period, which is comparable in other species of the family Sulidae, probably results from a very low metabolic rate. It certainly cannot be a function of egg size, since even the egg of the Ostrich requires only 42 days of incubation. One pair of boobies that I checked twice daily incubated an infertile egg for 63 days before finally ridding the nest of it. The fertility rate, as determined by tracing the natural fate of 86 eggs and examining all eggs that failed to hatch, was 90.7 per cent.

Both sexes of the Red-footed Booby incubate the single egg, and neither develops a brood patch that I could detect. At 11:12 a.m. on March 12, Female 22 laid an egg. I recorded her every move until she finally settled back and began incubation at 1:46 p.m. ---just two hours and 34 minutes later. She remained on the egg until after I left at dark, and the male was on the nest at five o'clock the following morning.

Table 6 summarizes my observations regarding the proportions of total time spent in incubation and attention to the young by males and females. I interpret the data in the following manner: The sexes share incubation time and time attending the young about equally, but the female spends longer at the nest before the egg is laid than the male does. The latter apparently results from two things. First, the female remains by the nest to perform the construction while the male gathers nest materials; and, second, the female spends up to three straight days on the nest just prior to, during, and shortly after laying.

In addition to keeping records of the total amount of time each sex spent at the nest, I noted which sex was on the nest each time I passed without remaining to observe for a long period. The "spot checks," as I called them, indicate the same general pattern of attention at the nest by the sexes as is indicated in the time table; however, the spot checks and time totals for each individual pair do not indicate the same results in every case. The spot check method of determining which sex spends longer at the nest is probably adequate if enough records are taken on several pairs.

While incubating, the birds frequently held the egg between their feet with the inner web of each foot stretched around the egg; occasionally only one foot was held against it. As a bird settled to incubate, it worked its egg up among the feathers of its belly. After it was settled, it usually remained fairly quiet for long periods of time. At irregular intervals it stood up for a few minutes, continuing to shade the egg, and

	Pre -egg	Incubation	Nestling	Totals
Male 21		39/03	57/27	96/30
Male 22	12/42	47/03	3/30	63/15
Male 23		44/05	31/12	75/17
Male 29		44/47		44/47
Male T39			35/45	35/45
Totals	12/42	174/58	127/54	315/34
Female 21		35/53	33/03	68/56
Female 22	40/51	48/07	3/25	92/23
Female 23		12/32	42/50	55/22
Female 29		58/56		58/56
Female T39			57/12	57/12
Totals	40/51	155/28	136/30	332/49

Table 6. Total time in hours and minutes (hours/minutes) that either sex was observed at the nest before the egg was laid, during incubation, and after the egg hatched.

then settled once more to incubate. During the heat of the day the incubating bird sat or panted or slept---now and then in a ridiculous position with its head hanging over the edge of the nest---, turning the egg infrequently or merely touching it with its bill. Incubation duties seemed to bore the birds, and they often passed the time by biting at small branches and leaves near the nest or by picking at the nest. I found that males and females alike would catch sticks I threw toward them, often nearly tumbling off the nest in an effort to get sticks thrown out of their reach. All the sticks they caught were added to the nest, and males often performed the stick-wave display with their catch.

Stretching the wings backward and the head and neck forward and "yawning"---gape opened wide, head frequently shaken---were common activities of birds on the nest. My data indicate that, as a rule, each bird sat for about 24 hours without interruption. Occasionally a bird was replaced after only about 12 hours of incubation, and I believe that some actually remained on the nest for 36 and 48 hours without a break. I saw two exchanges at the same nest in the same day only seven times in 648 nest-hours of observation (one hour observing five nests is equivalent to five nest-hours). In five of those cases, the exchanges occurred about twelve hours apart; in one case, about seven hours apart; and in the last instance only 17 minutes apart!

Throughout incubation the members of a pair saw little of one another except when one returned from fishing to replace the other on the nest. Frequently, after the female relieved the male at the nest,

the male spent some time gathering nest materials and bringing them back for the female to place. I never saw adults feed each other; apparently they go without food for as long as they incubate at one time. The nonincubating partner usually roosted away from the nest. In cases I knew of, the night roosts were from 10 to 25 feet from the nests of the pairs involved, and each pair had but a single night roost. Nest exchange, which usually occurred in the late afternoon or early evening, was simple and without ceremony. One bird flew in from its day of fishing, and the sitting bird immediately stood up and shifted to the edge of the nest or to a perch. The returning bird quickly took over at the nest, and its mate flew off. On a very few occasions the returning bird had to crowd the other off the nest. My records, corrected to compensate for different lengths of time spent observing at different times of the day, show that 20 exchanges between 5:00 and 7:00 a.m. compare with 13 between 7:00 a.m. and 3:00 p.m., eight between 3:00 and 5:00 p.m., and 48 between 5:00 and 7:00 p.m. I also have records of 55 exchanges that occurred between the last nest check in the evening and the first check in the morning. Many of those certainly took place after dark. The records included pairs still incubating and pairs attending young, and the general temporal pattern of exchange seemed to be the same in both cases. However, after the young had enough down to afford them protection from the sun, the adults left them alone at the nest for part of the day.

Care of the Young.

Young boobies began pipping the egg up to a full day before they finally freed themselves from the shell. Every hatched egg I examined had the blunt end removed as a cap, and apparently the adults simply dropped the pieces of the shell over the side of the nest. Newly-hatched Red-footed Boobies had pinkish-flesh colored skin with a dark gray or bluish-black area on the dorsum over the synsacrum. The eyelids and face were dark gray to grayish-brown; the bill was blackish-brown; and the feet and legs were flesh-colored. The eyelids were closed, though slit for about $3/16$ of an inch; and the irides were pearly gray. All feather tracts had ensheathed down; that on the back and on the alar and caudal tracts was not over $1/16$ of an inch long, and the remainder was not over $1/32$ of an inch long.

The color of the skin darkened gradually to gray; and by the time the young was eight days old only the neck was still slightly flesh-colored. Also by the eighth day most of the down had "bloomed" from the sheaths, and the young appeared sparsely down-covered. However, the down did not provide a satisfactory covering at that time. The birds were about two weeks old before they had enough down to give them any protection, and even then many areas were still virtually naked. My notes on the plumage of one young booby eighteen days old read "completely down-covered, though only sparsely on the throat and behind the eyes."

Feeding was by regurgitation, a process in which the adult opened

its mouth and the young introduced its bill into its parent's throat.

Maynard (1889) wrote the following about this species' manner of feeding the young at the Cayman Islands: "The newly hatched Gannets are fed at first by true regurgitation, that is the fish eaten by the parents is converted into a peculiar glairy fluid which is given to the young. The old birds introduce the terminal portion of the bill into the mouths of their offspring and the liquid is literally poured down their throats."

I find it difficult to believe that an adult introduced its bill into the mouth of its offspring! Newly hatched boobies have such small mouths that I doubt that they could accommodate enough of an adult's bill to permit the passage of food. I have sat in the colony at Half Moon Cay and taken notes as I observed the birds' activities; and, in 206 recorded feedings involving young of all ages, it was invariably the young bird that put its bill far into the adult's mouth. I suspect that Maynard neglected to record his observations in the field, and when he later wrote of the habits of this species his memory was confused on that point.

Feeding of the young was nearly confined to the late evening, occasionally it occurred in the early morning and apparently only rarely during midday. I recorded 2.6 feedings per each ten hours of observing between 5:00 and 7:00 a.m., none between 7:00 a.m. and 3:00 p.m., 7.8 per each ten hours between 3:00 and 5:00 p.m., and 30.4 per each ten hours between 5:00 and 7:00 p.m. From dawn to dark on April 26, I observed and recorded the activities of 13 pairs with young, and the first feeding I noted that day occurred at 5:48 p.m. Although I never observed

midday feedings, I know they must have occurred. Two young birds were repeatedly weighed in the morning and evening; in 23 such pairs of weighings I noted an increase in weight during the day on three occasions. I believe that feeding time is a very close function of the flight return periods of the adults, since the adults usually fed their young immediately after returning to the nest from a fishing excursion. And, since most birds fished all day and returned to the colony in the evening, most feeding of the young occurred in the evening. The graphs in Figure 9 illustrate a remarkably close correlation between the increase, peak, and decline in birds returning to the colony in the evening and the increase, peak, and decline in the incidence of evening feedings. The feeding observations were made on 32 days, and the flight return counts were taken in four evenings ---none of which coincided with evenings on which feeding observations were made. Nevertheless, I feel that the temporal sequence of activities of the boobies was invariable enough from day to day to make the above comparison significant. Of course, since the times of sunset differed considerably between the taking of the first records and the last, the figures should be combined on the basis of the peak periods of activity. However, both sets of figures were affected similarly by the differences in sunset time; so the adjustment seems unnecessary for this comparison.

There seemed to be only one feeding period per day, usually in the evening as noted above, for each young. There may be more occasionally, but I never observed more than one a day for any nestling. The

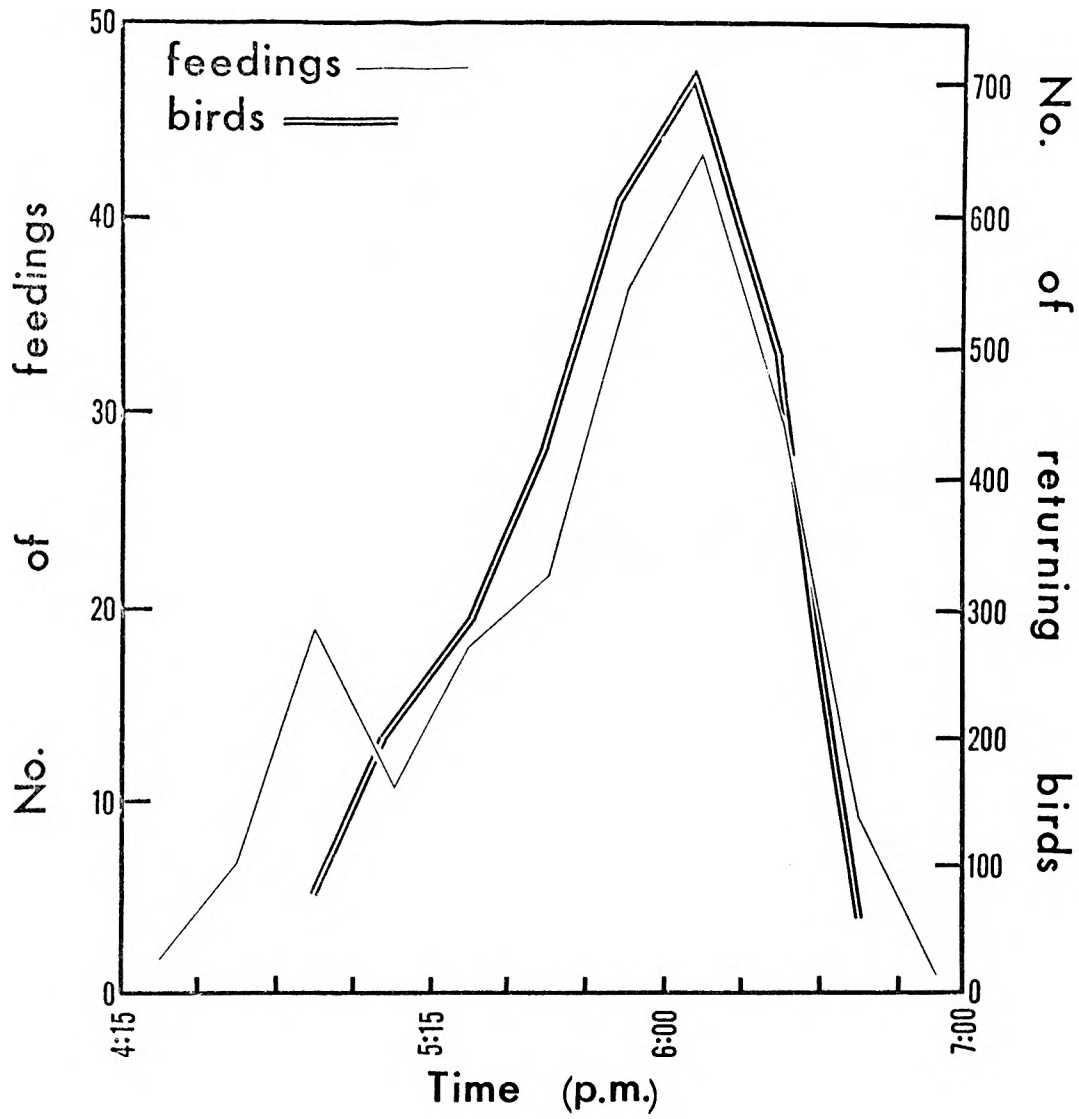


Figure 9. Comparison between the number of birds returning to the colony in the evening and the number of times young were fed during a comparable period.

young were frequently fed several times and sometimes by both parents during one feeding period, however. Both adults fed their young during the same period only after the nestling was old enough to be left alone part of the day, so that both parents could return to the nest from fishing at approximately the same time. In most cases the young was fed five or fewer times per feeding; although in an extreme case one female fed her young sixteen times in twenty minutes! Fortunately I had weighed the young just before the feedings; so I weighed it again just after and noted a weight increase of 62.9 grams as a result of the sixteen feedings.

When a young booby was hungry, it went through a regular routine of display before the adult that began with an incessant series of short notes that sounded like 'awp, awp, awp, awp.' The young bird doubled its neck up and held it back so its chin rested on its neck. In that position it rocked its head from side to side while "awping" and occasionally flailing its wings out to either side. Finally it began to jab at the base of the adult's bill, sometimes striking very hard. The adult responded either by turning its head away to avoid the young's blows or by opening its mouth and feeding the young. Sometimes a nestling simply "awped" and jabbed at the adult's bill, and sometimes the adult fed the young without any prompting at all. Usually the adult lowered its head enough to allow the young to reach far back into its throat. Out of the 35 occasions the sexes were distinguished, females were noted feeding the young during five more periods than males.

What I called "false feedings" were frequent and seemed to be a

response on the part of an adult to the agitation of its hungry young. During false feedings, the adult did not lower its head; therefore the young could get its bill only to the back of its parent's mouth. The adult did not gulp after false feedings as they did after genuine feedings, inasmuch as there was no food passed and nothing remained in the adult's throat to be swallowed. One of the most comical things I ever saw was two nestling boobies, one a "foster child," agitating to be fed by the same adult. The adult was flanked by the young birds, and each was jabbing at the base of the adult's bill. The old bird's head went from side to side, but it could not avoid the deluge of blows from both sides. So it finally opened up, and each young bird tried to get its head into the parent's mouth. Only one succeeded, however, and the adult left after the feeding.

Young boobies continue to depend on their parents for food long after they are able fliers; one juvenal that was flying a month before I left the colony was still returning to the old nest site each evening to receive food from its parents. In one extreme case, I observed a juvenal from the previous nesting season---certainly nearly a year old---being fed by one member of a pair that had their nest right behind my observation platform. I observed the feeding only once, but I suspected it had occurred several times before that. The juvenal flew in to land beside the old birds' nest nearly every evening, and even after their nest was broken up and the adults deserted the territory the juvenal returned to the spot. It was after the loss of the nest that I observed the feeding; thus the adult involved had to return to the original territory. It did so

just long enough to feed the juvenal. How long young ones must depend on the adults for food I do not know.

During the day, nestlings were a constant source of entertainment to me. When they were awake they sat on the nest and panted, fought with small branches and leaves by the nest, or flopped their wings around and bit at their own wrists. They liked to catch sticks I threw to them or try to take hold of the sticks the male brought in to be added to the nest. Nestlings often made life miserable for their parents by jabbing them or biting their wings and tails. When they slept they curled up on one side, laid on their stomach with their wings and neck stretched out to hang where they might, or even fell forward into a three-pointed stance on both feet and the top of their head. After a young booby was three or four weeks old, its parents ordinarily left it alone for a part of the day. As the young aged, the adults tended to leave it earlier in the day until, by about the tenth week, it was commonly left unattended for as many as 12 successive hours. Although the adults exhibited a tendency to leave their young earlier and earlier in the day, they seemed to return at about the same time each evening.

Young birds began exercising their wings long before they could fly. Their first attempts at flight were mainly extended hops on out-stretched wings, and they usually strayed far from their home territories during such trials. They became fully capable of flight before they lost all their down, and some were seen flying around with down still clinging to the sides of the neck and the top of the head. The last place to lose its

down was the forehead, and the brown juvenals carried that mark of their age for several days after they were capable fliers.

My notes on the development of young Red-footed Boobies are incomplete, since it takes longer for them to attain the juvenal dress than the twelve weeks I was in the colony at Half Moon Cay. In fact fourteen of the 221 nests I traced throughout my study had young on the nest when I arrived that still were not through the post-natal molt and could not fly when I left! However, I supplied Gilbert Saunders with a number of sheets on which he could check the various stages of development through fledging of the young boobies. He continued to check 11 nests, once a week, for more than four months after I had left Half Moon Cay. His data indicate that fledging requires from 13 to 16 weeks after hatching. There is a definite indication that the later the egg hatched the more rapidly the young developed. Four of the young apparently took close to 15 weeks to fledge, one took 16 weeks, and three required only about 13 weeks. All of the last three were hatched during the last five days in April; the others hatched during the first 13 days of April. I was unable to determine from Saunders' records how long three of the young took to fledge.

Eighty-one of the 221 nests mentioned earlier had flying young when I left, 83 had natals, and 57 had been broken up. Fifty-five of the losses were among the egg-containing and empty nests; so only two--- 2 per cent---of the 98 nests containing young were broken up. Therefore, if 2 per cent of the 83 nests containing natals when I left were eventually

lost, 81 of those nests would be successful. A grand total of 162 successful nests out of 221 yields a 73 per cent nesting success.

SUMMARY AND CONCLUSIONS

For three months I was engaged in an investigation of the nesting behavior of the Red-footed Booby (Sula sula) on Half Moon Cay, British Honduras. Since this species inhabits only isolated islands in the tropics, extended studies of the birds are difficult; as a result no one had ever before undertaken such a study. The data resulting from my study are, for the most part, new.

Half Moon Cay, a 45-1/2-acre coral island, lies 50 miles east of Belize on Lighthouse Reef. Coconut palms grow on most of the cay, but ground plants and shrubs have all been cleared from the eastern half. The boobies utilize an extensive stand of broadleaf trees in the southwestern section. Only one mammalian species occurs there; many birds, mostly migratory, were observed; and several species of lizards were recorded. The climate is mild and very uniform, especially during the months of the study period.

Certain features of the flight and reproductive behaviors of the boobies were studied in detail; data on plumage development are incomplete and have not been discussed in detail.

There were an estimated 3500 nonnestling red-footed Boobies in the colony, of which only 2 per cent were in the brown phase. Except at the height of their breeding cycle, it was impossible to distinguish sexes on the basis of their appearance.

Feeding flights left the cay early in the morning and returned late in the evening. Average flight unit size was 2.41; distinct flock patterns were not observed, and birds in flocks were not synchronous in their activities. Wind direction and force notably affected the birds' mode of morning departure but little affected their direction. They could fly from the ground unaided by wind.

Apparently the male selected the small territory, which was used for nesting, copulation, and occasionally roosting. Territorial defense was by threat display or vicious physical contact. Nestless pairs maintained territories at least three months; one such pair copulated regularly for at least a month.

Pair-bond maintenance differed in nestless pairs and nesting pairs.

Nests were normally circular and averaged 306 mm. in diameter. Average nest height was 18.4 feet, and average density was 126.7 nests per acre. Apparently the female initiated nest construction, after which the male gathered all materials while the female placed them. Nests were added to throughout incubation and after the egg hatched; the lining was changed occasionally during incubation; so the condition of lining leaves is not a good index to the stage of incubation of an egg. Thievery of nest materials was a common practice dictating that at least one member of a pair guard the nest at all times.

Just a single egg was laid per clutch at Half Moon Cay; some birds relaid after losing an egg. Fertility rate was 90.7 per cent; nest success

was approximately 73 per cent.

Incubation began shortly after laying (2 hrs., 34 min. in one case) and was shared about equally by the sexes. Exchange usually occurred in the evening, and the birds sat for 24 hours without interruption or food. No brood patch was found; incubating birds usually clutched the egg between their feet. Incubation periods averaged 44-1/2 days.

Young hatched helpless, with pinkish-flesh colored skin, and with ensheathed down on all tracts. They were fed by regurgitation by both adults during a single feeding period per day-- usually in the evening. Their development was extremely slow, and they continued to depend on the adults for food until long after they could fly. One bird nearly a year old was observed receiving food from a nesting adult. After the young were three to four weeks old their parents left them alone part of the day. Shortly before they could fly most young dismantled their nest and spent the remainder of their 'nestling' period on a perch.

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BIOGRAPHY

Jared Verner was born in Baltimore, Maryland, on August 16, 1934; shortly after that he moved with his family to Moscow, Idaho. He graduated from Washington State College with a degree of Bachelor of Science in wildlife management in 1957. He is a candidate for the degree of Master of Science in May, 1959.

EXAMINATION AND THESIS REPORT

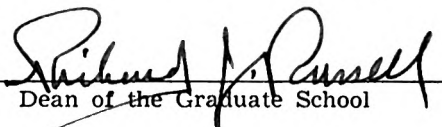
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Major Field: **Zoology**


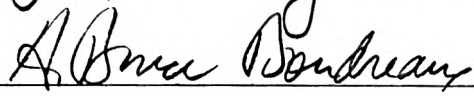

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Major Professor and Chairman


Dean of the Graduate School

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